

A STUDY OF VARIATION IN IONIC BALANCE  
AND ORGANIC ANION CONCENTRATION CAUSED BY  
K, Na, Cl, AND  $\text{SO}_4$  NUTRITION AFFECTING  
THE GROWTH AND DEVELOPMENT OF POTATO PLANTS

by

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Plate 1. General view of experiment 5 at Bush Estate Midlothian. Plots stand out but the colour differences are caused mainly by rate of N.



Plate 2. Close up photographs taken with exposures adjusted automatically by photocell and only minutes apart. On the left is treatment by KCl and right  $\text{Na}_2\text{SO}_4$ , both with 112 kg/ha of N. Mature plants in experiment 5.





Plate 3. General views of the same two plots shown in plate 2 with KCl on the left and  $\text{Na}_2\text{SO}_4$  on the right. The paler coloured and larger leaves resulting from KCl treatment are just visible in the photographs.



Plate 4. The same two plots as in plate 3 taken at senescence. The labels in these photos are placed at the front and not rear as in plate 3. Note the more advanced maturity of the left hand plot treated with KCl.





Plate 5. General view of the 'cage' at E.E.S.C.A. where experiments 2 and 6 were grown in boxes of sand: vermiculite. The pump unit for delivering nutrient solutions was later installed permanently inside the building. Note the control box front-left.



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Plate 7. Close-up views of the boxes used for experiments 2 and 6 and the wire mesh which was installed in 1966 after severe wind damage. Plants later grew normally through the mesh as in Plate 8 below. Boxes featured are the second



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Plate 9. A complete set of treatments in expt 8. 4 shoots were grown per pot of quartzite supplied regularly with nutrient solutions. In the centre is a control; from it the K:Na ratio increases as  $\text{SO}_4^{2-}$  to the left and  $\text{Cl}^-$  to the right.



Plate 10. A closer view of the pots in plate 9 with the control in the centre and the pure salts which were (L to R)  $\text{K}_2\text{SO}_4$ ,  $\text{Na}_2\text{SO}_4$ , control, NaCl and KCl.





Plate 11. View of the pots in experiment 9 immediately prior to harvest. The 2 pots on the left are the soil of low  $K^+$  status, and on the right high  $K^+$  status. The extreme left and right hand pots are the controls compared with  $Na_2SO_4$  supplied to the centre 2 pots.



Plate 12. In the left hand photo are pots of low  $K^+$  status soil and in the right hand are the pots of high  $K^+$  status soil (Expt 9). In both cases the 3 pots represent treatment from left to right with pure  $K_2SO_4$ ,  $\frac{1}{2} K_2SO_4 + \frac{1}{2} Na_2SO_4$  and pure  $Na_2SO_4$  respectively. Notice severe foliar  $K^+$  deficiency symptoms when  $Na_2SO_4$  was supplied to the  $K^+$  deficient soil. N deficiency also is apparent.

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1,3 GLOSSARY

Most scientific terms used in the text have their normally accepted meaning and usage; this glossary defines certain terms used in the text rather more specifically.

Absorption - total quantity of an ion (= content) absorbed by the whole plant or a morphological region of it.

Allometric ratio - a simple arithmetic function describing the relationship between 2 characteristics (gen. of 2 plant regions) during ontogeny (cv).

$\Sigma A$  = sum of inorganic anions - stoichiometric total of free  $\text{NO}_3^-$  and  $\text{SO}_4^{2-}$ , total P as  $\text{H}_2\text{PO}_4^-$  and  $\text{Cl}^-$ ;  $\text{SO}_4^{2-}$  values are calculated as described in 5,2,3.

$\Sigma C$  = sum of cations - stoichiometric total of  $\text{K}^+$ ,  $\text{Na}^+$ ,  $\text{Ca}^{2+}$  and  $\text{Mg}^{2+}$ .

(C-A) - difference between  $\Sigma C$  and  $\Sigma A$  known to be stoichiometrically = organic anions of volatile plant acids; significant in control of internal pH during anabolism of N and S and differential absorption of C and A.

Concentration treatments/series - a set of treatments in which the salt concentration (cation and anion together) is varied in supply.

Exchange effect - used by Henderson (1965) to denote the difference between  $\text{K}_2\text{SO}_4$  and KCl fertilisers at the same rate of  $\text{K}^+$ .

Fertilisers - sometimes used in the text as abbr. of KCl,  $\text{K}_2\text{SO}_4$ , NaCl and  $\text{Na}_2\text{SO}_4$  or combinations of them,

$\text{K}_{\text{max}}$  - quantity of fertiliser  $\text{K}^+$  required to maximise yield calculated from the fitted equation  $y = a + bx + cx^2$ .



$K_{\text{soil}}$  - exchangeable  $K^+$  status of the soil in  $\text{Kg } K^+/\text{ha}$ .

$(N+S)_0$  - organic N and S (mono-and divalent respectively)  
representing total anabolised ions with electron transfer.

Ontogeny - the progressive change with time in morphological  
or ionic characteristics in a plant as a function of age.

R - used to denote 1. value of KCl as % of  $K_2SO_4$  in  
chapter 3, 2. allometric ratio (cv) between foliage and  
tuber ions.

Relative absorption coefficient  $\alpha_{12}$  - a measure of the  
propensity of a plant species to absorb more of one ion  
than another relative to the ratio of their concentration  
in the supply.

Relative crowding coefficient  $K_{12}$  - a measure of the inhibiting  
effect during absorption of an ion by another of the same  
charge.

Replacement/treatment series - a set of treatments in which  
a cation (or anion) species is progressively replaced by  
another with the maintenance of stoichiometric total  
constant in the supply.

1,4 GENERAL SUMMARY

The study began as an investigation of the cause of the tendency of  $K_2SO_4$  compared with KCl to produce a similar total yield but a larger ratio of the seed to ware fractions of the potato crop. It was postulated initially that the effect on size distribution was due to  $K_2SO_4$  producing more aerial stems with greater tuber potential but the same sized photosynthetic system; the same amount of assimilate would be distributed between more tubers. Assuming it to be inert,  $Na^+$  was introduced as a replacement for  $K^+$  to isolate the effect as being due to the anions alone or to the salts.

Some growth and chemical analysis data are presented from:

1. a series of 25 NPK, type of K manurial trials on potatoes in S.E. Scotland in 1966, at 9 of which stems were counted to test the alternative hypothesis that the effect is independent of stem number,
2. growth analysis field experiments in 1966 and 1967 comparing the effects of KCl and  $Na_2SO_4$  on the morphological and ionic ontogeny of potatoes,
3. a field trial in 1966 to test the interaction of 4 salts with rate of N and stem number,
4. controlled environment experiments, 1 using soil and 5 using artificial medium fed periodically by nutrient solution of which 2 were grown to maturity under a 'cage' and 4 of short duration in a greenhouse.

From the results of the 25 manurial trials it was concluded that the original premise was true only on soils of

certain  $K^+$  status. On  $K^+$  deficient soils (defined as those with high values of  $K_{max}$ , the amount of fertiliser  $K^+$  to maximise yield) KCl was superior for yield and produced a smaller seed/ware ratio than  $K_2SO_4$ . On  $K^+$  sufficient soils the reverse was true. The association of yield superiority with smaller seed/ware ratio was termed a 'more perfect  $K^+$  nutrition' syndrome. Models were defined to describe the effects. The effects in relation to  $K^+$  status were <sup>more</sup> pronounced on sandy, freely drained soils and less on heavy, imperfectly drained soils than the models predicted. At current prices KCl was shown to be superior for seed production on  $K^+$  deficient and  $K_2SO_4$  <sup>on  $K^+$</sup>  sufficient soils. The threshold of about 260 kg exchangeable  $K^+$ /ha would be greater on light and less on heavy textured soils.

At 8 out of 9 sites  $K_2SO_4$  produced more aerial stems than KCl by an average of 4.4%, some evidence to support the corresponding effect, observed in a pot experiment, of much greater pre-emergence shoot necrosis and axillary branching. With more stems,  $K_2SO_4$  was expected to produce more tubers and a greater seed/ware ratio than KCl. At these sites plants were selected with the same number of stems on both treatments and at harvest revealed that  $K_2SO_4$  increased the seed/ware ratio independently of any effect on stem number, compared with KCl. However, the data from the whole plots harvested at these sites revealed that in fact they were all of high  $K^+$  status and as such  $K_2SO_4$  produced smaller not greater seed/ware ratios than KCl. It is not easy to explain the discrepancy between the expected and the actual result.



The ontogeny and distribution of ions in potatoes grown at 2 sites; 1 of high  $K^+$  and low  $Mg^{2+}$  status and the other the reverse, were studied in relation to the theories of ionic balance, based on excised roots and once-only sampling of plants without a dominant 'sink'. Within the plant as a whole the anabolism of N and S was closely related to the synthesis of organic anions, but they were unrelated in the leaves alone due to the selective withdrawal of organic N and S and accumulation of the  $Ca^{2+}$ , and less so  $Mg^{2+}$ , salts of organic acids. The organic anions were translocated mainly as  $K^+$  salts but on the low  $K^+$  soil,  $Mg^{2+}$  substituted in this role. With time, leaf concentration of N, S and  $K^+$  markedly decreased and  $Ca^{2+}$  increased and yet a plateau occurred during the period of tuber bulking in the concentration of organic anions. The latter in the tubers stabilised at the same level at both sites. It appears that the theories of ionic balance linked to growth are not invalidated by the development of a 'sink'.

From a review of literature it was concluded and calculated that,

1. it may not be possible to distinguish between anion and salt effects,
2.  $K^+$  may be delivered more rapidly to the roots by diffusion from the KCl than from  $K_2SO_4$ ,
3. the main influences on ionic absorption will be Donnan phenomena in the root cortex,
4. more  $K^+$  and  $Cl^-$  will be absorbed from KCl than  $K^+$  and  $SO_4^{2-}$  from  $K_2SO_4$ ,

5. substitution of  $K^+$  by  $Na^+$  in supply will cause the absorption of more divalent cations rather than  $Na^+$ ,
6.  $K^+$  and  $SO_4^{2-}$  will be selectively absorbed from mixed salts,
7. potatoes may respond to more available  $K^+$  from KCl but at high rates may suffer from the consequences of reduced concentration of organic anions and reduced internal pH.

The replacement of  $Na^+$  by  $K^+$  in supply resulted in the predicted increased selectivity towards  $K^+$  absorption, inhibition of  $Na^+$  absorption and the substitution of divalent cations for  $K^+$  in the absorption pattern. The substitution was not stoichiometric,  $\Sigma C$  increased more than  $\Sigma A$ , and organic anion concentration increased in consequence. Selectivity favoured the absorption of  $K^+$  from mixtures with divalent cations and  $Mg^{2+}$  from a mixture with  $Ca^{2+}$ . Thus a 3 cations competitive system during absorption exists in potatoes between  $K^+$ ,  $Ca^{2+}$  and  $Mg^{2+}$ .

The replacement of  $SO_4^{2-}$  by  $Cl^-$  resulted in the predicted increase in selectivity towards  $SO_4^{2-}$  but  $Cl^-$  inhibited  $SO_4^{2-}$  absorption. Very much more  $Cl^-$  was absorbed than  $SO_4^{2-}$  when these ions were equally supplied and the differential significantly increased through the season. The replacement had the predicted effect in reducing the concentration of organic anions but in the experiments studied it was insufficient to stress the system and substantially affect growth. This replacement in short-term experiments resulted in the predicted greater absorption of  $K^+$  but in experiments

grown to maturity and sampled nearer senescence the reverse tended to occur. The replacement resulted in the greater absorption of divalent cations throughout. This change with time in the relative equilibrium tissue concentrations in the leaves may be due to the enhanced deposition of divalent cations, mainly as the salts of organic acids, and their close reciprocal relationship with  $K^+$  concentration, where  $Cl^-$  is the dominant anion in supply. The features of the effect suggest the more rapid attainment of physiological maturity on  $Cl^-$ .  $NO_3^-$  was selectively absorbed from mixtures with  $Cl^-$  and  $SO_4^{2-}$  but  $H_2PO_4^-$  was unaffected so that in potatoes a 3 anion competitive system seems to exist. More  $NO_3^-$  was absorbed when the dominant treatment ions in supply were  $Na^+$  and  $SO_4^{2-}$  (when  $K^+$  was not deficient).

There is evidence that KCl compared with  $K_2SO_4$  increases the metabolic rate of the parent tuber, increasing water absorption and the rate of shoot growth but producing greater apical dominance and less axillary branching; the effect observed was related to the effect of  $K_2SO_4$  in increasing the rotting of tubers and necrosis of the shoot-tips. Compared with  $Na_2SO_4$  but also with  $K_2SO_4$ , KCl produced greater leaf area early in the season and this may be related to the production of a greater weight of stolons and the initiation of more tubers, the differentials being lost later in the season. This effect of KCl on leaf area may be responsible for the effect on leaf chlorophyll which may be diluted by deposition of more assimilates. There was little evidence of a close relationship between the organic anion concentration

and growth except in a pot experiment in which extraneous  $K^+$  was almost eliminated and yield of tubers was maximised by the mixtures of  $K^+$  and  $Na^+$  in supply. The N response in a field trial was associated with a large increase in organic anion concentration in the leaves.

In quality tests, KCl significantly reduced mealiness and tendency of tubers to disintegrate during cooking. This may be related to the effect of KCl in increasing succulence of leaves and tubers compared with  $K_2SO_4$  (and  $Na_2SO_4$ ) in a manner similar to the effect of increased rate of  $K^+$ . The association of the 2 effects is not new but this study provides evidence from other measurements in support of the hypothesis.

These observations may be related to the syndrome of 'more perfect  $K^+$  nutrition' from KCl than  $K_2SO_4$  particularly on sandy and freely drained soils of low  $K^+$  status by proposing that the effect is one of the delivery and absorption of more  $K^+$  from KCl, at least initially. The reversal of the effect on heavy soils of high  $K^+$  status may be related to the effect of KCl compared with  $K_2SO_4$  in reducing the organic anion concentration in the foliage and stressing the internal pH control mechanism.

INTRODUCTION

Sodium chloride has long been established as a valuable supplement or replacement potash fertiliser for many root crops. It was war time however which forced British farmers to reconsider their established prejudice against muriate of potash for potatoes. It was on potatoes, the heaviest consumer of potash per unit of crop after sugar beet, that the dilemma posed the greatest problem. Russell and Garner in 1941 were followed by Cowie in 1943 in admitting that the use of KCl on potatoes as <sup>a</sup> substitute for  $K_2SO_4$  carried the attendant expectation of reduced total yield. Other work and conflicting results followed but by the early 1960's one fact had become firmly established; whereas KCl may not produce a lower total yield it tends to increase the proportion of large and reduce the proportion of small tubers in the crop. A series of trials conducted in England and Scotland culminated in papers by Dickins et al (1962), Simpson and Crooks (1965) and Henderson (1965) on the subject of replacement of  $K_2SO_4$  by KCl, all reporting the same effect on size distribution.

It was against this background that this study began in 1965. Its objective was to identify the mechanism by which  $K_2SO_4$ , relative to KCl, affected the size distribution of the tubers in the crop without influencing total yield. Throughout the study the key hypothesis was that  $K_2SO_4$ , relative to KCl, increased the metabolic rate of the seed tuber and caused more primary buds to develop and more axillary branching below the soil surface. Evidence was already available (for example Bremner and El Saeed, 1963) that the number of tubers



at harvest varied directly and average tuber weight indirectly with the number of stems per unit area of the crop. The effect of treatment was anticipated to be initially biochemical but thereafter a purely physical consequence of distributing the assimilates of the same effective leaf area and efficiency between more tubers. The fact that a potato plant initiates many more tubers than ultimately are harvested required that resorption should be strictly proportional to the number of tubers initiated and to the number of stems in order that the hypothesis should be true. It became clear that resorption is a delicate physiological balance and an area which is amenable to treatment effect. Whether or not there was a mechanism influencing the number of stoloniferous stems it was foreseen that initially  $K_2SO_4$  may be nutritionally more satisfactory than KCl, a larger 'source' establishing a larger 'sink', the latter initially being measured in number of tubers. Subsequently the nutritional balance may change in favour of KCl and the smaller 'sink' is supplied from a larger 'source'. Such a mechanism in which the ontogenetic change of 'source' is influenced by treatment could be demonstrated only by growth analysis.

Meanwhile, another question had arisen; was the effect due to the anions or to the cation and anions in combination? This debate persisted throughout the experimental period of the study leading eventually to generalisations about the significance of individual elements and the balance between cations and anions within the potato plant. It was known

that  $\text{Na}^+$  is not absorbed in more than tiny quantities by the potato plant and as such it was seen as a useful vehicle for the supply of  $\text{Cl}^-$  and  $\text{SO}_4^{2-}$  for comparison with  $\text{KCl}$  and  $\text{K}_2\text{SO}_4$ . It was late in the study that chemical analysis revealed the greater uptake of  $\text{Ca}^{2+}$  and  $\text{Mg}^{2+}$  to balance the uptake of  $\text{Cl}^-$  and  $\text{SO}_4^{2-}$  supplied as the  $\text{Na}^+$  salts, and by implication the importance of cation-anion balance.

At the end of the study a third hypothesis belatedly emerged to explain the exchange effect of  $\text{KCl}$  and  $\text{K}_2\text{SO}_4$ . The clue had been given many years previously by Terman et al (1953) and subsequently by Harrap (1960). In both papers the similarity between the effect of  $\text{KCl}$  relative to  $\text{K}_2\text{SO}_4$  and the effect of increasing rate of fertiliser  $\text{K}^+$  in reducing the percentage dry matter in the tubers was reported. Since the effect of increasing fertiliser  $\text{K}^+$  undoubtedly was due to the increased uptake of  $\text{K}^+$  it was recognised that the  $\text{KCl}:\text{K}_2\text{SO}_4$  effect could be due to the relatively greater uptake of  $\text{K}^+$  from  $\text{KCl}$ . Indeed Schmalfluss and Reinicke (1960) and Udovenko et al (1964) for example without remarking on its significance demonstrated that this was the case.

Realisation that the relative effect of  $\text{KCl}$  may be the manifestation of effectively a greater rate of applied  $\text{K}^+$  provided new scope for the interpretation of the many effects which  $\text{KCl}$ , compared with  $\text{K}_2\text{SO}_4$ , was observed to have.  $\text{K}^+$  was known to have little effect on E except in late season though it increases L (Watson and Wilson, 1956; Humphries and French, 1961).  $\text{K}^+$  was said to increase leaf size from an early stage (Van der Paauw, 1940; Ward, 1959) by increasing



leaf expansion (Fernando, 1958). Evidence for  $K^+$  effect on stem and tuber number is conflicting (Emmert, 1946; Ward, 1959; Ivins, 1963; Henderson, 1965) but its effect on increasing the proportion of large tubers irrespective of a yield increase is generally recognised (eg Simpson and Crooks, 1961; Dickins et al, 1962; Ivins, 1963).

The results of the experiments proved to be not entirely consistent with this hypothesis for one obvious reason that KCl seems to be more 'toxic' at high rates and at high soil  $K^+$  status than  $K_2SO_4$ . Therefore the alternatives are not completely rejected in the interpretation which follows.

There were 2 serious difficulties to be overcome in this study. Firstly, the effect was not entirely consistent and secondly the effect was very small when differences in yield of seed and ware sized tubers were compared with total yield. Thus the effect might be described as 'statistical' emerging out of the average of a number of trials. As such the effect is not really amenable to the in-depth study, involving comprehensive growth and chemical analysis, of a single trial. The result was something of a proliferation of trials in both controlled environment and field individually bearing little hope of producing an unequivocal answer. In fact the only organisationally useful discovery to be made was that  $Na_2SO_4$  exhibited to a greater extreme the properties of  $K_2SO_4$  as a <sup>t</sup>ertiliser. This simplified the growth analysis trials, which are very demanding of resources, by permitting the comparison of KCl with  $Na_2SO_4$  in the hopes of a more prominent effect.

As it was, the first growth analysis trial was poorly designed and the samples too small. The second suffered badly from severe drought and, inadvertently in the light of subsequent knowledge, poor siting with respect to the soil  $K^+$  status. It was not until the results of a large series of routine potato manurial trials conducted in 1966 were examined in detail at the end of the study that the possible reasons emerged for inconsistency and to a certain extent smallness of effect. Had this information been available earlier, most certainly it would have changed the course of the study. So important are the consequences of this information to the interpretation of the results of the study that although strictly not part of it, they are presented and discussed as section 3 before the results of the study itself. The actual chronological order and synopsis of the trials is given below.

#### Winter 1964/65

1. Greenhouse. Expt. to compare the effect of KCl and  $K_2SO_4$  on tubers sprouting in pots of sand.

#### Summer 1965

2. Cage. Potatoes grown to maturity in boxes of sand: vermiculite with treatments supplied weekly in solution. 3 ratios K:Na x 3 anions (Cl,  $SO_4$ ,  $SiO_3$ ).

#### Winter 1965/6

3. Greenhouse. Potatoes grown for 10 wks in pots of sand: vermiculite with treatments supplied weekly in solution, 3 ratios of K:Na x Cl: $SO_4$ .

## Summer 1966

4. Growth analysis trial in field (Harperdean, E. Lothian), high  $K^+$  status soil. Treatments control, KCl and  $Na_2SO_4$  sampled 3 weekly.
5. Demonstration expt. Bush Estate. Crop grown to maturity. Treatments 3 rates of N x 4 combinations KCl,  $K_2SO_4$ , NaCl,  $Na_2SO_4$  x 2 stem no.
6. Cage. Similar to Expt. 2 with  $SiO_3$  treatment dropped and size increased.
7. Imposed on 10 of the routine manurial trials. 1 plant with each of 2, 3 and 4 stems in every plot labelled and harvested separately. (7B) Stem counts made within all plots of one trial and totalled over KCl and  $K_2SO_4$  in remaining 9.

## Winter 1966/7

8. Greenhouse. Single sprout cores grown for 12 weeks in pots of sand and treated weekly with treatments in solution. 5 ratios of K:Na and 2 anions Cl and  $SO_4$ .
9. Greenhouse. Selected tubers grown for 11 weeks in pots of 2 soil types treated with 3 ratios K:Na and anions Cl: $SO_4$ .

## Summer 1967

10. Growth analysis trial in field (Meadowhead, Edinburgh), med  $K^+$  status soil. Treatments as Expt. 4 but large samples and better layout. Badly affected by drought.
11. 4 field trials to assess commercial replacement value of K salts by Na salts for potatoes.

This study began early in 1965 and a sequence of experiments was conducted until the summer of 1967. In all there were 11 experiments in the study some being repeated at several sites. Concurrently in 1966 an extensive series of 25 routine manurial trials was conducted in S.E. Scotland as part of which KCl was compared at 3 rates with  $K_2SO_4$ . With chemical and morphological analyses, the quantity of data produced was enormous. The bulk of this was punched with instructions on paper tape and sent to Rothamsted Experiment Station to be run with their Simplex, Genfac and Genfac II programs. This was barely completed before the author transferred to the Ministry of Overseas Development in 1968. After a period of secondment overseas during which the study was suspended by the Faculty of Science Postgraduates Committee, the author returned to UK in 1974. Thus after a lapse of 6 years the study was reinstated. Work continued from December 1974 during study leave generously granted by the Civil Service Department and the Director of Land Resources Division of the Ministry of Overseas Development.

### 3 THE RESULTS OF FIELD EXPERIMENTS WITH KCl AND $K_2SO_4$ ON POTATOES

#### 3,1 THE EFFECT ON TOTAL YIELD

##### 3,1,1 Introduction

Discussion of the relative merits of the sulphate and chloride forms of potash fertiliser for potatoes has appeared in a number of papers. Conclusions tend to be either that the sulphate is superior to the chloride form in increasing total yield or that there is no difference in total yield merely a consistently greater reduction by KCl of the seed/ware ratio than by  $K_2SO_4$ . A third conclusion has emerged perhaps rather tentatively in recent years that in certain situations KCl may be superior at low rates of application but  $K_2SO_4$  superior at high rates. However, several authors conclude that there is little evidence to support this observation. From the mean effects of  $K^+$  as KCl and  $K_2SO_4$  from a number of potato trials in S.E. Scotland in 1966 grouped by soil series it was clear that the situation might be more complex than hitherto it had been considered. It is the object of this section to examine the possible reasons for the conflicting evidence.

The discussion began with the change from  $K_2SO_4$  to KCl as the main sources of potash in agriculture during world war II. The chloride ion was considered to be toxic when applied at high rates to horticultural crops. Russell and Garner (1941) estimated the potato yield reduction compared with the  $SO_4^{2-}$  to be 5 cwt per 1 cwt of chloride applied. Dickins et al.



(1962) suggest that this estimate may reflect yield reduction from NaCl, a contaminant in the muriate of potash in use at the time. However reports of the superiority of  $K_2SO_4$  for total yield production range from then until more recent times (Russell and Garner, 1941; Cowie 1943; Vazhenin, 1951; Gething, 1959; Corbet and Gausman, 1960; Henderson, 1965; Kampfer and Zehler, 1967). Summaries of series of trials are reported by Cooke (1961), Dickins et al. (1962), Timm and Merkle (1963), Simpson and Crooks (1965) and Gething (1968) in which it was concluded that although there were cases which significantly demonstrated the superiority of one or other of the potash types, on balance the effects cancelled. Laughlin (1966) reported 2 trials in which the comparative effects of the 2 sources on total yield was opposite in successive years. More recently Grison and Fourbet (1973) concluded that  $K^+$  as the 2 forms increased yield equally but Shuglya (1974) found that out of 4 types of potash it was kainit which increased yield by the greatest amount.

In 1959, Gething noted the evidence that the superiority of  $K_2SO_4$  was more marked with increase in rate of  $K^+$ . However, the first appearance in the literature of a meaningful rate x form of potash interaction was in a review by Harrap (1960). By 2 small inset graphs he indicated that the yield response to KCl is more strongly quadratic than that to  $K_2SO_4$  whether or not the linear coefficient is in the same order. The consequence of this idea is that at high rate of  $K^+$ ,  $K_2SO_4$  inevitably is the superior source. From the failure of the mean over sites rate x type of  $K^+$  interaction to attain

significance Dickins et al. (1962) concluded that rate did not influence the exchange effect. However the trend was there. Summarising 11 trials in 1962/3 Gething (1968) concluded that there was no real indication that relative performance was related to rate. However, in the same paper he concludes from a 1963/4 series in which a second method of application was introduced into the experiment, that whereas  $K_2SO_4$  produced a lower yield at low rates it produced a higher yield at high rates. More recently, Kämpfer and Zehler (1967) and Johansson (1973) (summarising the results of 68 trials in Sweden) arrived at a similar conclusion. Henderson (1965) also noticed the tendency for  $K_2SO_4$  to outyield KCl to be more marked at higher rates but decided against any real trend being demonstrated. He comments " This paucity of interaction (between rate and form of  $K^+$ ) can hardly be regarded as conclusive however, since the ranges of rates were rather limited. Much variation in the exchange effects seems to have been due to intersite factors, but there is no satisfactory way of identifying those primarily involved." Comparing his results on mainly seed crops with those of Dickins et al. (1962) on ware crops he suggests that the exchange effect may be influenced by the general level of tuber size in the crop. The major determinants of tuber size such as seed size and spacing and haulm destruction may interact with the exchange factor and so vary its effect.

The total yield results quoted by Henderson (1965) tend to fall into 2 groups on the magnitude of the  $K^+$  response ( $K_2-K_1$ ). The mean response of these groups is shown in



table 3,1,1 together with the equivalent mean superiority of  $K_2SO_4$  over KCl.

Table 3,1,1: Data of total yield response in tons/ac from

Henderson (1965)

|                               | $K_2-K_1$ | $K_2SO_4-KCl$ |
|-------------------------------|-----------|---------------|
| negative $K^+$ response group | -0,16     | 0,43          |
| positive " " "                | +0,44     | 0,33          |

From the series 1 results quoted by Dickins et al. (1952) a similar exercise reveals a similar trend. In fig. 3,1,1 the  $K_3-K_1$  affect in tons/ac is plotted against the  $K_2SO_4 - KCl$  effect. Out of 16 sites 5 have been omitted because the quadratic coefficient between  $K_1$  and  $K_3$  is positive. Of the remaining 11 sites there is one clear outlier, Sandiway 1960. Omitting that site too, the resultant correlation of  $r = 0,63$  is significant at  $P = 0,05$ . Although from the citric acid extracts of soil  $K^+$  there appears to be no relationship between  $K^+$  response and soil  $K^+$  status, one might assume that in keeping with the generally accepted relationship between soil nutrient status and crop response to that nutrient (for example Lucas (1968), table 6),  $K_3-K_1$  may be substituted by an inverse exponential scale of soil  $K^+$  status. On that basis the relationship in fig. 3,1,1 suggests that a point may be reached in terms of soil plus fertiliser  $K^+$ , above which the relative merits of  $K_2SO_4$  and KCl become reversed. Such a model would appear as in fig. 3,1,2.

Fig. 3,1,1: Relationship of response to K to the relative effect of KCl and  $K_2SO_4$  (from Dickins et al. (1962)).

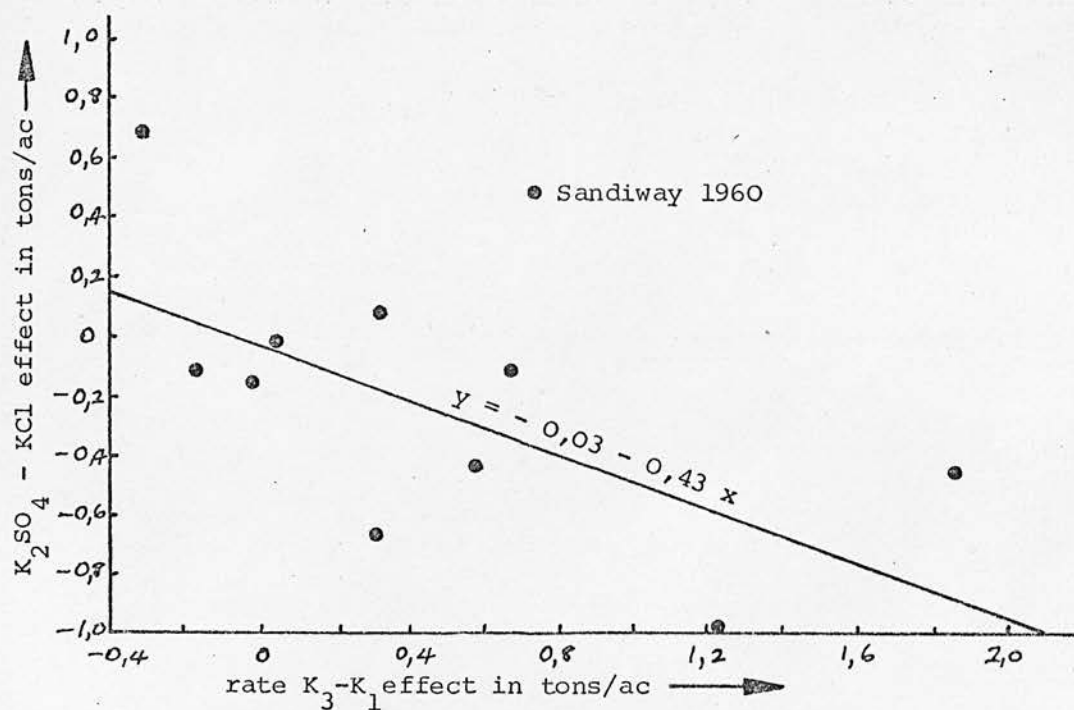
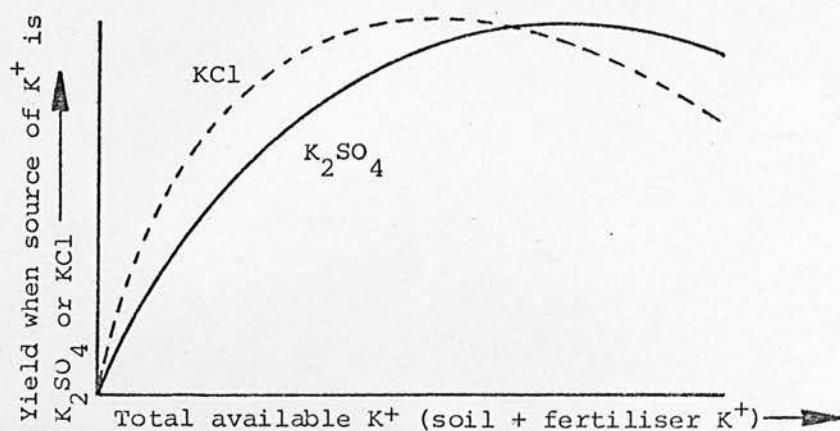


Fig. 3,1,2: Model relating effect of rate of KCl and  $K_2SO_4$  on total potato yield at different levels of total available potassium



### 3,1,2 Experimental

In 1966 the Soils Department of Edinburgh School of Agriculture conducted a series of 25 standard potato manurial trials mainly in the counties of Angus, Perth, Fife, Midlothian and East Lothian. The design compared factorial combinations of 3 rates of N and  $K^+$  and 2 rates of P within 2 blocks on which were imposed a type of  $K^+$  comparison, KCl and  $K_2SO_4$ . Complete details of the trials are given in appendix 10,2. These trials were distributed as evenly as possible between 5 important soil series, each site being selected to be as close as possible to the type profile of the series while retaining as much objectiveness in 'randomisation' of sites as possible. The 5 soil series may be ordered approximately on texture and drainage as in the table below:

| soil series | no. of sites |
|-------------|--------------|
| Vinny       | 3            |
| Forfar      | 4            |
| Balrownie   | 7            |
| Macmerry    | 6            |
| Winton      | 5            |

Heaviness of texture and impence of drainage increase down the table (Grant, 1975).

### 3,1,3 Results

The total yield results measured over N and P rates are given in full in appendix 10,3. The level of  $K^+$  fertiliser required to maximise yield at each site ( $K_{max}$ )

was calculated. Several authors prefer the quadratic  $y = a + \sqrt{bx} + cx$  to  $y = a + bx + cx^2$  for fitting to fertiliser /yield response curves but when only 3 points are to be fitted the choice of equation is immaterial. Thus the linear and quadratic coefficients of the main effect of  $K^+$  rate at each site were calculated and from them the values of  $K_{\max}$  (appendix 10,4,1 ). The value of  $K_{\max}$  is known to vary with absolute yield. Holliday (1963) concludes from a series of potato trials in Wales and W. Midlands that high yielding soils have a higher  $N_{\max}$  when the N status of the soil is low than low yielding soils (when N is the limiting nutrient of any species). To arrive at this conclusion the author used the yield at high fertiliser rate as an index of absolute yield. The yield at  $K_{\max}$  would be the best index in this study but to save time on calculation the actual yield at  $K_1$  has been used in this exercise (see appendix 10,4,1 ). The adjusted values of  $K_{\max}$  are given in appendix 10,4,2 and with them the index of the relative performance of KCl and  $K_2SO_4$ , the mean total yield of the former as a percentage of the latter. A plot of these values is shown in fig. 3,1,3.

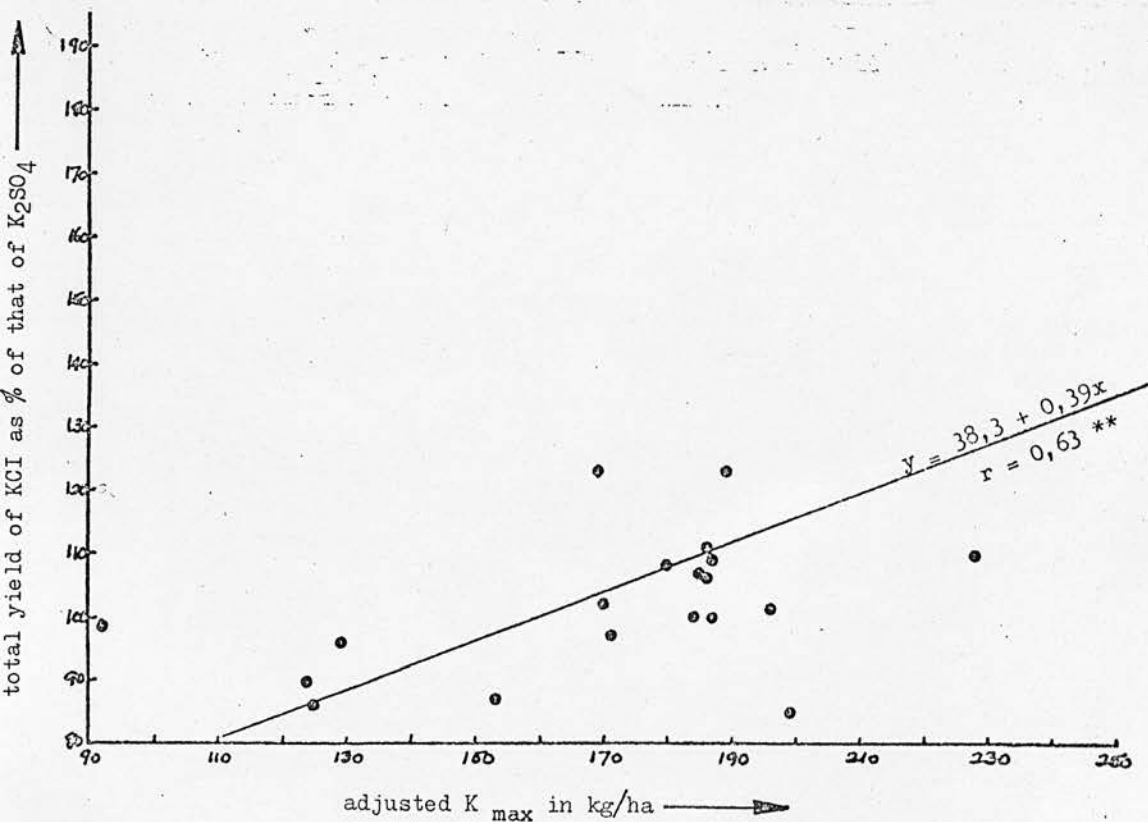
The regression (shown in fig. 3,1,3) and the correlation  $r = 0,63$  were significant at  $P = 0,01$ .

### 3,1,4 Discussion

The regression shown in fig. 3,1,3 is highly significant which is surprising in view of the poor estimate of the relationship of the main effects of KCl and  $K_2SO_4$ . The type

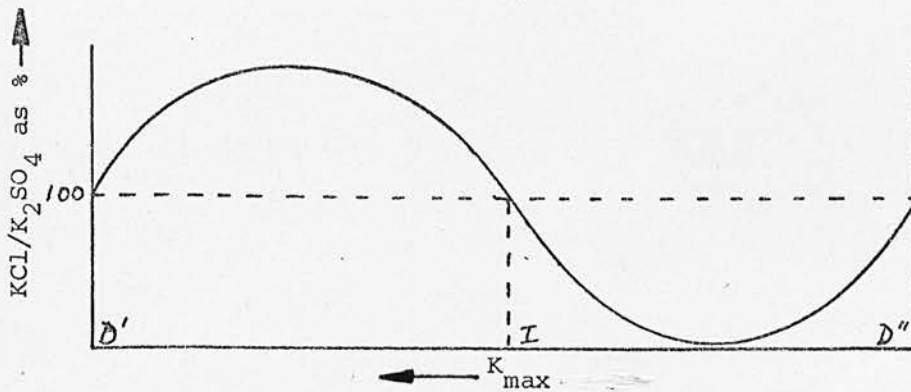


Fig. 3,1,3: Relationship between the level of fertiliser K required to maximise yield and the relative effects on total yield of KCl and  $K_2SO_4$ .



of potash factor was comfounded with blocks at each site, each block with 18 plots covering a wide area and being subject to the full impact of any environmental trend. A linear regression has been fitted but the model would require a cubic fit had a full range of  $K_{max}$  values been obtained. Redrawing the model in terms of KCl as a percentage of  $K_2SO_4$  and  $K_{max}$  it would have the form of fig. 3,1,4.

Fig.3,1,4: A model relating yield of KCl and  $K_2SO_4$  with  $K_{max}$ .



At an infinitely large value of  $K_{max}$  ( $D'$ ), the available  $K^+$  would be 0 and yield would be 0. As  $K_{max}$  decreases the yield from KCl increases more than that from  $K_2SO_4$  and the ratio exceeds 100 to reach a maximum and decrease to the point of inflexion (I). Above this level of available  $K^+$ ,  $K_2SO_4$  becomes the superior source and the ratio reaches a minimum before rising again to 100 at the point  $D''$  where available  $K^+$  is so great as to be toxic and prevent growth. Thus only the region around the point of inflexion can be regarded as linear. This suggests that the range of available  $K^+$  levels tested in this series of trials was small compared with the range from 0 to that which would cause complete crop failure. This accords with the fact that  $K_1$  was 101 kg/ha of  $K^+$  and  $K_3$  was 235 Kg/ha and the range small by comparison with that used, for example by Hahlin and Johansson (1973).

It has been assumed that  $K_{max}$  follows a simple relationship with available soil  $K^+$ ; such as

$$K_{soil} = a + K_{max}^{-b} \dots\dots\dots(1)$$

Reports vary in the extent to which response by potatoes to fertiliser  $K^+$  is related to the conventional measures of soil available  $K^+$  status. For example Edwards (1956), Simpson and Crooks (1961), Holliday (1963), Timm and Merkle (1963), Birch et al. (1967), Lucas (1968), Surarex (1970), Ekeberg (1972), Gregory (1972) report some success in predicting  $K^+$  requirement from soil analysis but in contrast Dickins et al. (1962) and Simpson et al. (1973) found little evidence of a relationship. Boyd and Dermott (1964 and 1967) in contrast to Dickins et al. (1962) conclude that soil groups accounted for the major part of intersite variance in  $K^+$  response due mainly to their contrasting soil texture. Soil  $K^+$  status was strongly related to soil texture so that soil analysis accounted for very little variance after allowing for soil texture. The table in appendix / 10,4,1 shows the tendency for the mean  $K_{max}$  values within soil series to fall as texture becomes progressively heavy and drainage impeded, from Vinny to Winton series.

The dependency of  $K_{max}$  upon the level of other factors for example upon the level of available N and P is demonstrated in the reports of Boyd (1961), Boyd and Dermott, (1964) and Simpson and Crooks (1961). Thus intersite variation in level of native N and P and indeed the availability of applied N and P clearly will effect the estimates of  $K_{max}$ . The amount of animal manure applied to the site also will effect response, directly by increasing the amount of available  $K^+$  other than from fertiliser. Boyd (1961) showed that even when response in the presence of manure is compensated by its  $K^+$  content,

interaction with the N and P it contains can occur.

Thus previous cropping history and other soil factors influence the simple relationship between crop response to applied  $K^+$  and the chemical extraction of soil  $K^+$ . However, this influence should be seen as causing deviations from the simple relationship without necessarily modifying its basic form. The  $K_{\max}$  points in Fig. 3,1,3 tend to cluster around the range 160 to 200 kg/ha. If these are adopted as arbitrary limits the sites fall into three groups on the basis of  $K_{\max}$ ; 'low' with 5 sites of mean 125 kg/ha, 'medium' with 13 sites of mean 184 kg/ha and 'high' with 2 sites of mean 242 kg/ha. If the high mean is assumed to correspond to an available soil  $K^+$  content of 80 kg/ha and the 'low' mean to a content of 350 kg/ha then the exponent in equation (1) can be estimated and the equation becomes

$$K_{\text{soil}} = 2323 - K_{\max}^{.941} \dots \dots \dots (2)$$

Solving the equation for the 'medium'  $K_{\max}$  mean of 184 kg/ha the equivalent soil  $K^+$  status is 192 Kg of  $K^+$ /ha. The relationship between the groups on a  $K_{\text{soil}}$  basis is shown in table 3,1,2

Table 3,1,2: Relationship between the  $K_{\max}$  groups.

| $K_{\max}$<br>group mean |     | estimated<br>$K_{\text{soil}}$ | difference |
|--------------------------|-----|--------------------------------|------------|
| high                     | 242 | 80                             |            |
|                          |     |                                | 112        |
| medium                   | 184 | 192                            |            |
|                          |     |                                | 158        |
| low                      | 125 | 350                            |            |

Thus although the  $K_{\max}$  group means are exactly evenly spaced, the equivalent  $K_{\text{soil}}$  values are exponentially spaced, the intervals being in the ratio  $\frac{158}{112} = 1.4:1$ .



The spacial arrangement of the three groups along the abscissa of the original model in Fig. 3,1,2 is now fixed. Although the means of the 2 sources of  $K^+$  are fixed with respect to each other within each site and within each group of sites by the data themselves the variation of the overall site or group mean is a variable of factors outside the control of the experiments such as husbandry, variety and spacing. However this variation legitimately may be incorporated in arbitrary constants fixed by the estimated value of soil  $K^+$  and to the group overall mean, the group mean response to  $K^+$  to KCl with respect to  $K_2SO_4$  and the interaction between them. These relationships may be formalised by defining the model.

### 3,1,5. Definition of model

When no fertiliser  $K^+$  is applied the total yield would be related to soil  $K^+$  status:

$$Y = c + dK_s - eK_s^2 \dots \dots \dots (3)$$

Substituting equation (1) in (3) an estimate of yield would be

$$c + d(a + K_m^b) - e(a + K_m^b)^2 + A \dots \dots \dots (4)$$

where a and b are constants relating soil  $K^+$  to  $K_{max}$  ( $K_m$ ), c, d and e are constants relating the yield to soil  $K^+$  status and A is the error of the estimate. Let this estimate of Y be that of the mean (R) of a set of T (type) x K (rate) data for a given value of  $K_{max}$ . Since the absolute value of R has not been specified, let it be standardised against another value (X) taken in this case to be the yield of level 1 of KCl in the 'low'  $K_{max}$  group. Thus the estimate of R is

$$fX^{-1} [c+d(a+K_m^b) - e(a + K_m^b)^2 + A] \dots\dots\dots (5)$$

where  $f$  is a constant relating the absolute values of  $R$  to the standard value  $X$ . Now the estimate of yield of a given rate of fertiliser  $K^+$  of a given type within a group, the mean of which is  $R$ , is

$$R + K' - k'' + t \pm tk' \pm tk'' + B \dots\dots\dots (6)$$

where  $k'$  and  $k''$  are the linear/<sup>and</sup>quadratic effects of rate of  $K^+$  and  $t$  is the contrast  $KCl$  versus  $K_2SO_4$  and  $tk'$  and  $tk''$  are the interaction effects.  $B$  is the error of the estimate.

Substituting (5) into (6) gives the estimate of a standardised yield of a given rate of fertiliser  $K^+$  of a given type at a given value of  $K_{max}$  of the group mean  $R$ :

$$fX^{-1} [c+d(a+K_m^b)-e(a+K_m^b)^2+A] + k'-k''+t\pm tk'\pm tk''+B \dots\dots\dots (7)$$

### 3,1,6. Proving the model

Using the trial results grouped as suggested above on the basis of  $K_{max}$  the values of  $k$ ,  $t$ ,  $tk$  and  $B$  can be calculated. If  $a$  and  $b$  are given the assumed values in equation (2) and  $f$  an arbitrary value then  $c$ ,  $d$ ,  $e$  and  $A$  can be estimated. If the procedure is repeated with systematic changes in  $a$ ,  $b$  and  $f$  a value of  $A$  can be estimated for each iteration. Limiting values of  $a$  and  $b$  can be fixed by the plausible limits of real soil  $K^+$  and arbitrary limits of  $f$ . The best model is that in which the estimate of  $A$  is minimal.

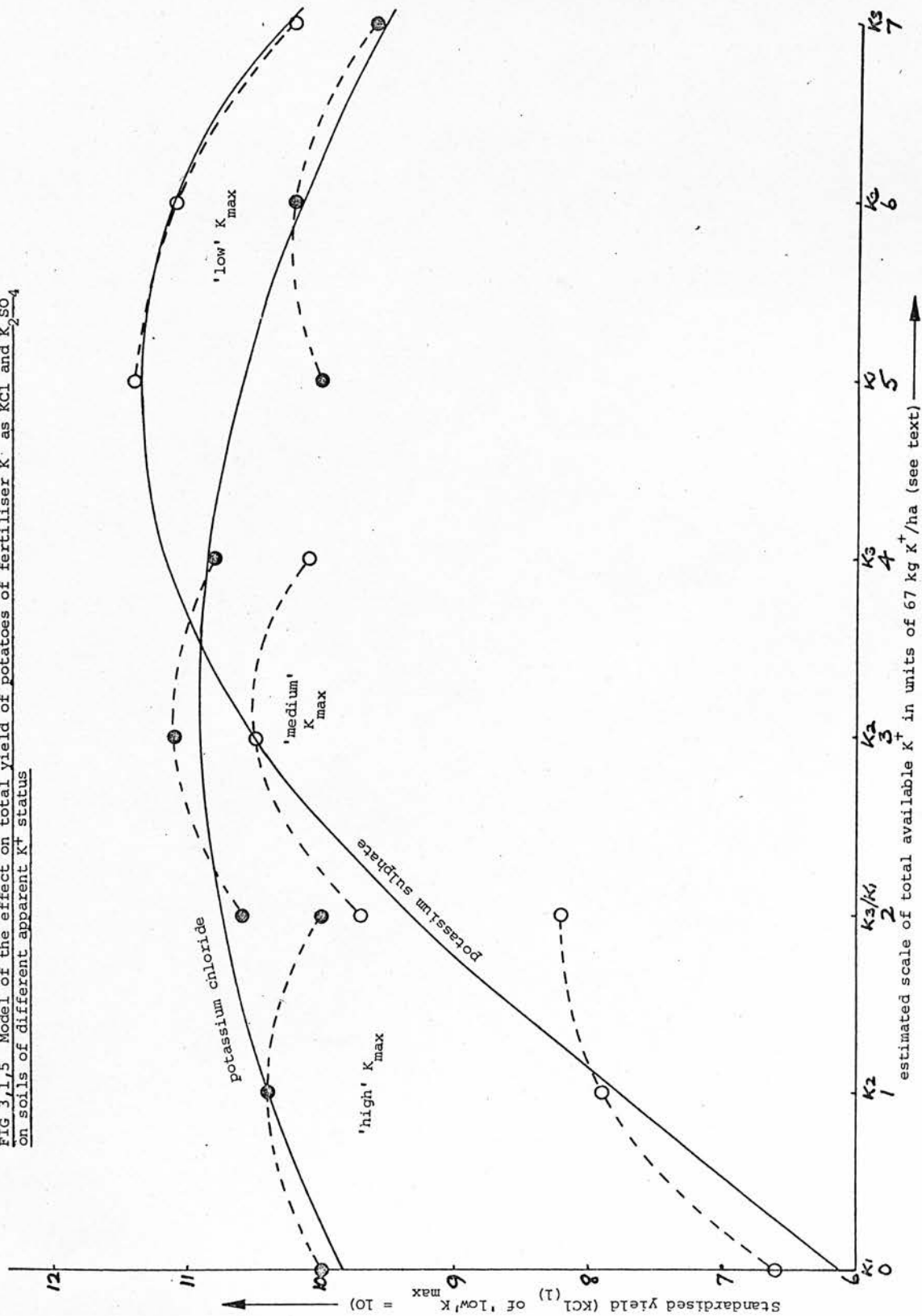
Clearly this is work for a computer. No facility was <sup>and</sup> available quickly/easily to the author so the exercise was completed 'by eye'. The values of  $a$  and  $b$  used were nearly those in equation (2) and in this case  $f$  was 10 for each group.

The result is shown in Fig. 3,1,5. The origin of the abscissa corresponds to an assumed level of soil  $K^+$  of 13 Kg/ha. The units of the abscissa are equivalent to 67 kg/ha of  $K^+$  of soil or fertiliser origin. Thus the cross-over of the response curves (drawn by eye) is at a level of total available  $K^+$  of 250 kg/ha of  $K^+$

One feature of the fitted model is the deviation of the high rate of fertiliser  $K^+$  of both types in the 'low' and 'medium'  $K_{max}$  groups. The most obvious explanation is that this level of potassium salt applied in a fairly concentrated band causes permanent damage. It is greater than the 200 kg  $K^+$ /ha reported by Simpson (1963) as damaging the roots of young potato plants. Gething (1968) demonstrated that the depressive effect of KCl compared with  $K_2SO_4$  could be partly alleviated by incorporating the fertiliser by rotary cultivator.

The effect of season on this model derived from trial data of 1 year only is speculative. The seed/ware ratios were abnormally high in most cases and this may be due to the dry July in summer of 1966 but the total yields generally are not particularly low. However, a suggestion by Gething (1968) in summarising the 1962/3 series of trials, that the relative effectiveness of KCl was greater in the drier eastern counties may anticipate a possible conclusion from future work that the cross-over point in an 'average' season may occur at a lower rate of available  $K^+$ .

FIG 3.1.5 Model of the effect on total yield of potatoes of fertiliser  $K^+$  as KCl and  $K_2SO_4$  on soils of different apparent  $K^+$  status





### 3,1,7. Summary of section 3,1.

Certain reported trials comparing the chloride and sulphate forms of potash reveal a possible relationship between the relative performance of the two fertilisers and the magnitude of response to  $K^+$ . If so this could partly explain conflicting conclusions regarding their relative merit. Selected data from 25 potato manurial trials in S.E. Scotland are shown to confirm this conclusion. Grouped on the basis of the fertiliser  $K^+$  required to maximise yield the data substantiate a model constructed to show the superiority of KCl on  $K^+$  deficient soils and that of  $K_2SO_4$  on  $K^+$  fertile soils.

## 3,2. THE EFFECT ON THE SIZE DISTRIBUTION OF POTATO TUBERS

### 3,2,1. Introduction.

Many authors on the subject of potassium response in potatoes have recorded or reported the tendency for increasing fertiliser  $K^+$  to increase the proportion of large tubers and generally reduce that of medium tubers (eg. Simpson and Crooks, 1961 and 1965; Henderson, 1965; Will, 1966; Kämpfer and Zehler, 1967; Hahlin and Johansson, 1973). An exception appears in the data of Dickins et al. (1962, table 5) in which the yield of medium tubers tended to increase with increasing rate of  $K^+$  and at a greater rate than that of large tubers; the ratio of medium to large tubers increased with  $K^+$ . The reason, Henderson (1965) suggests, may be the contrasting husbandry for mainly ware production in England and seed production in

Scotland.

In the same way that fertiliser  $K^+$  reduces the seed/ware ratio, the level of soil  $K^+$  may do the same. It can be deduced from the data of Simpson and Crooks (1961) that the seed ware ratio is reduced less by fertiliser  $K^+$  on soils of high than on soils of low  $K^+$  status. In another paper (Simpson *et al.* 1973) the site data can be grouped into those of low, medium and high  $K^+$  status. The seed/ware ratios are inversely related to the soil  $K^+$  status but for the purpose of comparing the effect of  $K^+$  the ratios may be standardised on the  $K_1$  value = 10 in each group. The mean seed/ware ratios and standardised values (in brackets) are shown in table 3,2,1.

Table 3,2,1: Calculated seed/ware ratios on soils of different K status (data from Simpson *et al.* 1973).

| Soil status | $K_1$    | $K_2$     | $K_3$    |
|-------------|----------|-----------|----------|
| low         | 2,86(10) | 2,03 (7)  | 1,52 (5) |
| medium      | 2,01(10) | 1,76 (9)  | 1,70 (9) |
| high        | 0,82(10) | 0,78 (10) | 0.63 (8) |

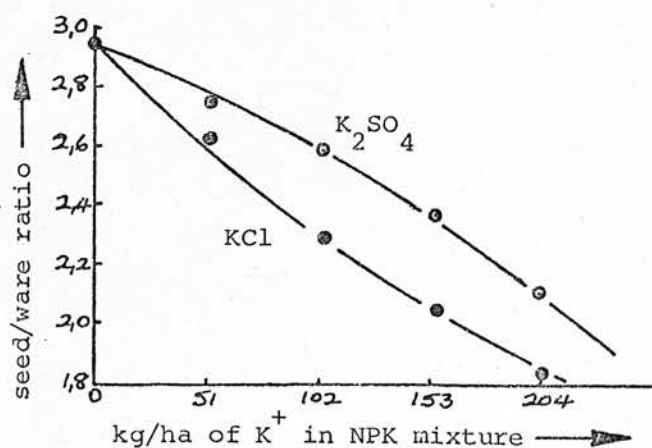
Again the trend is visible of the  $K^+$  status of the soil influencing the effect of  $K^+$  on the seed/ware ratio.

There is one feature which is consistent in all the reports of trials in which  $KCl$  and  $K_2SO_4$  are compared;  $KCl$  produces more large tubers than  $K_2SO_4$ . In the data of Dickins *et al.* (1962), Henderson (1965), Simpson and Crooks (1965) and Gething (1968) it is clear that there are exceptions to this generalisation. It is the object of this

section to examine the possible reasons for these exceptions. The emphasis is upon the ratio of the number of seed size tubers (32 - 57 mm) to the numbers of ware size tubers (>57 mm). The justification for this is given in appendix/10,4,2/. Average tuber weight is an insensitive measure of change in size distribution and like seed/ware ratio on a weight basis may produce an equivocal response to change in size distribution because the ware fraction has only a single size limit, that which distinguishes between seed and ware.

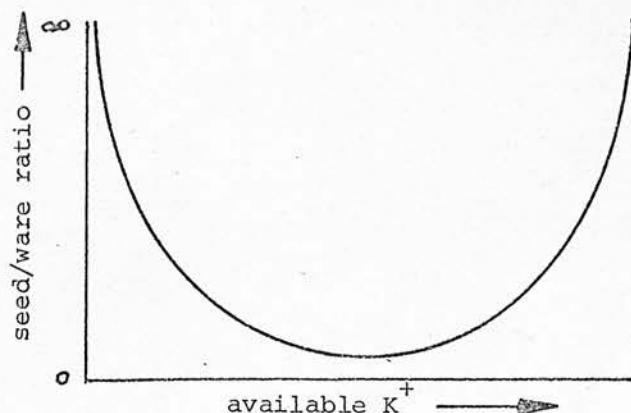
The data of Simpson and Crooks (1965) are plotted in fig. 3,2,1.

Fig. 3,2,1: Effect of KCl and  $K_2SO_4$  on seed/ware ratio (Data from Simpson and Crooks, 1965).



If these data are understood to imply that as conditions become more 'favourable', in this case due to improvement in  $K^+$  nutrition as yield responded to the highest level of  $K^+$ , then the theoretical relationship might be as in fig. 3,2,2.

FIG 3,2,2 Theoretical effect of available  $K^+$  on seed/ware ratio



In perfect  $K^+$  deficiency the seed/ware ratio was infinitely large (in fact it becomes so well above perfect deficiency), falls to a minimum at perhaps perfect  $K^+$  nutrition and rises to infinity as  $K^+$  becomes toxic. Thus the response to KCl in fig. 3,2,1 may represent a portion of the curve in fig. 3,2,2. However, the response to  $K_2SO_4$  in fig. 3,2,1 is negatively quadratic. In part this is due to the common origin of the 2 curves at nil fertiliser  $K^+$ . However, there is evidence of negative curvature between  $K_2$  and  $K_4$ . If quadratic equations are fitted then

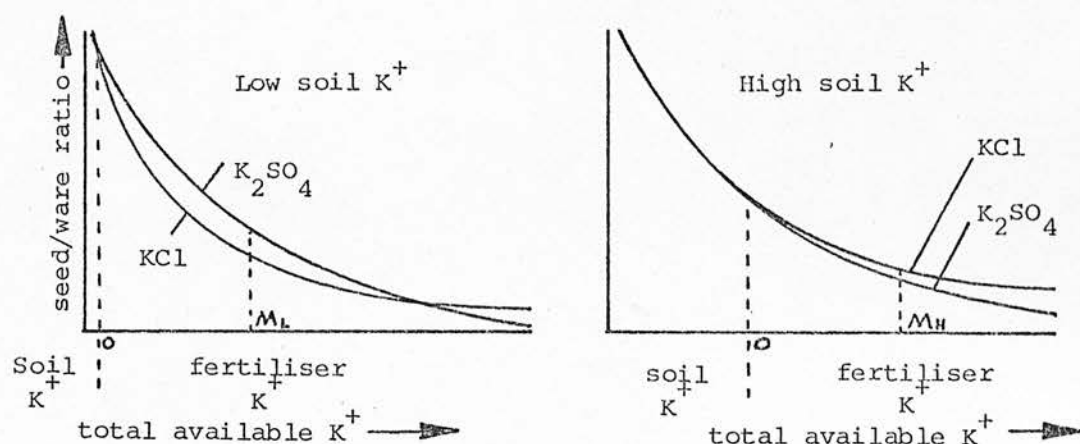
$$Y_{KCl} = 2,97 - 0,37K + 0,022K^2 \dots\dots\dots(1)$$

$$Y_{K_2SO_4} = 2,95 - 0,15K - 0,015K^2 \dots\dots\dots(2)$$

When equation (1) equals equation (2) the curves cross; solving the quadratic equation, the cross-over occurs at 298 kg  $K^+$ /ha.

From the evidence for the effect of soil  $K^+$  status and rate of fertiliser  $K^+$  on the effect of KCl and  $K_2SO_4$  then models can be constructed to describe their effect on seed/ware ratio. These are shown in fig. 3,2,3.

FIG 3,2,3 Models to show the effect of KCl and  $K_2SO_4$  on soils of low and high  $K^+$  status (see text)



In both models the cross-over occurs at the same level of total available  $K^+$  (soil plus fertiliser  $K^+$ ). When soil  $K^+$  is low then the cross-over occurs at a high rate of  $K^+$  fertiliser. When soil  $K^+$  is higher than the cross-over point in terms of total available  $K^+$ , then the curves produced by KCl and  $K_2SO_4$  have 'already crossed-over' as shown. At the mean level of fertiliser  $K^+$  in the low soil  $K^+$  model ( $M_L$ ) the seed/ware ratio of KCl is less than that of  $K_2SO_4$ . At the corresponding mean ( $M_H$ ) in the high soil  $K^+$  model the curves are reversed.

### 3,2,2. Experimental

The details of 25 trials in 1966 from which the following data are taken are given in section 3,1 and appendix 10,2,4.

### 3,2,3. Results.

By an exercise described in section 3,1 the level of fertiliser  $K^+$  required to maximise yield was calculated and adjusted for variation in absolute yield at each of 20 sites. Five sites were rejected because  $K_{max}$  could not be estimated.

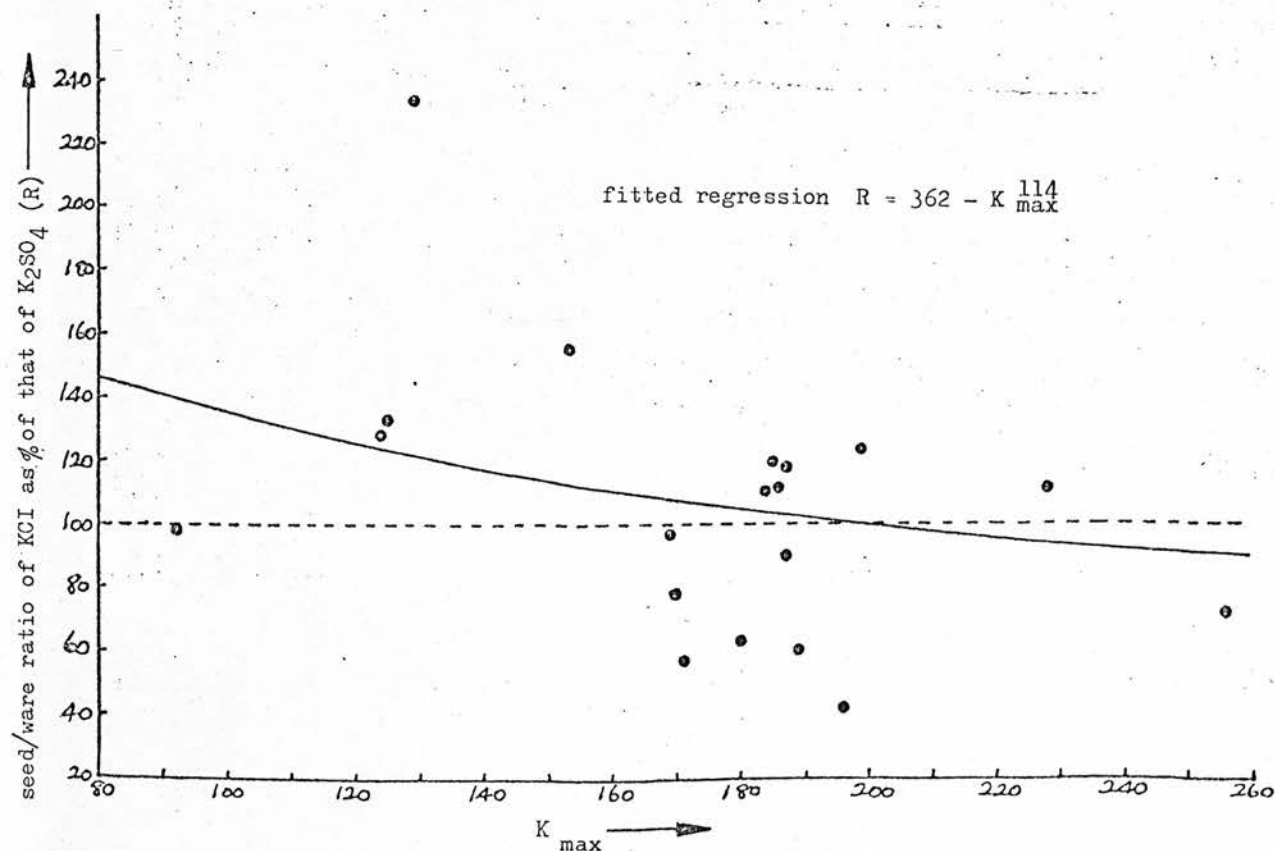


Against the values of  $K_{\max}$  the mean seed/ware ratios of KCl treatment as a percentage of those from  $K_2SO_4$  (R) are shown in appendix/10,4,2. The regression between R (number basis) and  $K_{\max}$  as the affecting variate was not significant at  $P = 0,05$ . Because the  $K_{\max}$  scale is considered to be an exponential index of soil  $K^+$  (see section 3,1) the response of R against  $\log K_{\max}$  was calculated. Accounting for 44% of the variation in R it almost attained significance at  $P = 0,05$  ( $F = 4,24$ ); it was

$$R = 362 - K_{\max}^{114}$$

A plot of R against  $K_{\max}$  and the fitted regression appears in fig. 3,2,4.

Fig. 3,2,4: Relationship of the relative effects of KCl and  $K_2SO_4$  on the seed/ware ratio (R) and the level of fertiliser  $K^+$  required to maximise total yield ( $K_{\max}$ ).



A plot of the deviations showed them to be strongly related to soil series and moreover, quantitatively related to increasingly heavy texture and impeded drainage. Ordered by these characteristics (see appendix/<sup>10,2,1</sup>) the series were scored as in table 3,2,2 below.

Table 3,2,2: Soil series scored for variation in texture and drainage.

| soil series | score |
|-------------|-------|
| Vinny       | 5     |
| Forfar      | 4     |
| Balrownie   | 3     |
| Macmerry    | 2     |
| Winton      | 1     |

The regression of R directly on the soil series score was highly significant and accounted for 63% of the variation in R; it was

$$R = 163 - 20,7 \text{ soil series score}$$

There was only a weak relationship between  $K_{\max}$  and soil series.  $K_{\max}$  was markedly lower in Winton series as might be expected and almost significantly so at  $P = 0,05$  ( $F = 4,28$ ), but overall soil series accounted for only 49% of the variation in  $K_{\max}$ . So it was not surprising that the multiple regression of R on  $\log K_{\max}$  and soil series score should account for more variation in R (70%) than either affecting variate separately. The highly significant regression ( $P = 0,01$ ) was

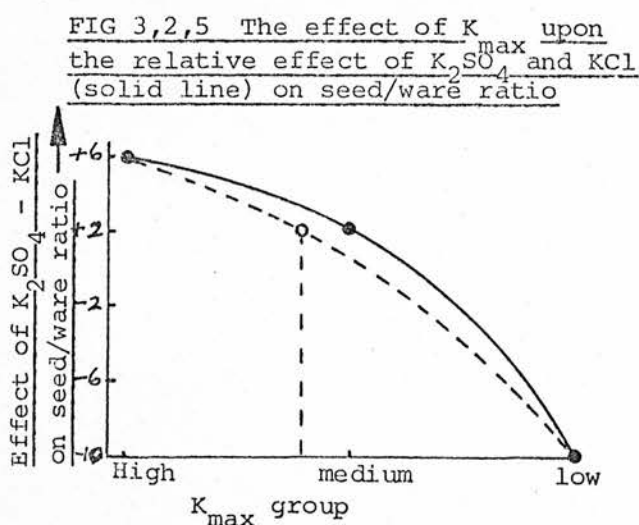
$$R = 342 - K_{\max}^{82} - 18,5 \text{ soil series score.}$$

As noted in section 3,1, random deviations from the regression should be expected because of the poor estimate of any contrast between KCl and  $K_2SO_4$ , the main effect of which was



confounded with blocks.

In view of the effect of rate of fertiliser  $K^+$  on the seed/ware ratio as described in the introduction then the main effect of type (for R is an alternative expression of the main effect of type) may be affected by its interaction with rate of  $K^+$ . The full treatments  $\times$  sites matrix of seed/ware ratios, is shown in appendix <sup>10,4,1</sup> and the variance within it may be analysed. The first problem is that of the selection of the error term. There are two possibilities, the pooled site errors and the residual variance within the matrix after removal of the required effects. Appendix <sup>10,4,3</sup> describes the polynomials required to estimate these effects and the method used to calculate pooled error and residual variance. The residual variance with a coefficient of variation of 50% was selected and the analysis of variance table is given. Only 3 effects attained significance and all were at  $P = 0,01$ . These were the main effect of rate of  $K^+$  reducing the seed/ware ratio and the linear and quadratic contrasts between the 3  $K_{\max}$  groups significantly changing the effect of KCl and  $K_2SO_4$ . This effect is shown in fig. 3,2,5 as the solid line.



As argued previously, the  $K_{\max}$  scale probably is an inverse,

exponential scale of soil  $K^+$  the 'medium' position on which is indicated by the dashed ordinate. The line redrawn on a soil  $K^+$  scale (dashed line) is still quadratic and a reason for this may be found in the absolute value of the group means. The 'low'  $K_{\max}$  group has a high mean seed/ware ratio whereas according to the model in fig. 3,2,3 it is expected to be the lowest. Since the magnitude of the effect is likely to be related directly to the absolute value of the mean then the effect in this group may be overestimated. With an adjusted value for the 'low'  $K_{\max}$  group, the effect of soil  $K^+$  on the relative effect of KCl and  $K_2SO_4$  becomes almost linear.

The problem created by the extraneous effect of site on the absolute value of the seed/ware ratio has been discussed at length in appendix <sup>10,4,4</sup> /. There are two main conclusions. Firstly, if adjustment for variation between sites is necessary then the adjustment should be exponential in view of the exponential relationship between seed/ware ratio and the husbandry and other factors which cause the variation. Secondly, if this kind of adjustment is made then the analysis on the raw data may have little in common with that on the transformed data. However, because adjustment between groups essentially is rather subjective a simple linear transformation has been made of the  $K_{\max}$  group means by standardising the values on level 1 of KCl. Raw and standardised (in brackets) values are shown in table 3,2,3 below.

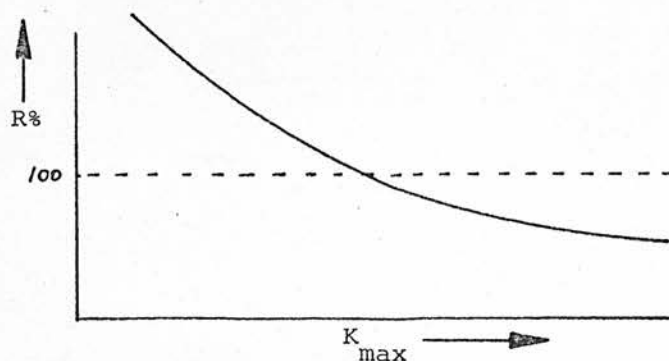
Table 3,2,3: The effect of rate and type of  $K^+$  and  $K_{\max}$  on the seed/ware ratio (and the standardised ratio in brackets)

| $K_{\max}$ group | KCl    |        |       | $K_2SO_4$ |        |       |
|------------------|--------|--------|-------|-----------|--------|-------|
|                  | $K_1$  | $K_2$  | $K_3$ | $K_1$     | $K_2$  | $K_3$ |
| low              | 28(10) | 27(10) | 25(9) | 18(6)     | 16(6)  | 16(6) |
| medium           | 19(10) | 14(7)  | 15(8) | 20(11)    | 19(10) | 16(8) |
| high             | 30(10) | 24(8)  | 18(6) | 35(12)    | 32(11) | 23(8) |

### 3,2,4. Discussion

In the model shown in fig. 3,2,3 of the effect of KCl and  $K_2SO_4$  fertiliser when soil  $K^+$  status is low the value of R is less than 100%. In the alternative model at high soil  $K^+$  status the value of R will be greater than 100%. Thus R is a positive function of soil  $K^+$  or a negative function of  $K_{\max}$  (see section 3,1). The model could be redrawn as in fig. 3,2,6 assuming  $K_{\max}$  to be exponentially related to soil  $K^+$  and the function of R on soil  $K^+$  to be linear.

Fig. 3,2,6: Model of the effect of  $K_{\max}$  on the main effect of seed/ware ratio of KCl as percentage of that of  $K_2SO_4$  (R)



The trial data plotted in fig. 3,2,4 using the same co-ordinates



show a marked resemblance to the model in fig. 3,2,6. Despite the large deviations expected from poor estimation of  $R$  at each site, the deviations were strongly related to soil type and apparently to soil texture and drainage. Where the soil was sandy and freely drained then  $R$  was well below the regression line indicating that  $KCl$  compared with  $K_2SO_4$  produced a low seed/ware ratio. From the description of fig. 3,2,2 this situation is understood to be a reflection of more perfect potassium nutrition. Some possible reasons for this effect are examined in the general discussion section 3,3.

The analysis of variance of the sites  $\times$  treatments data matrix should reveal large effects of the interaction of the main effect of  $T$  with soil series and  $K_{max}$  groups (in that order) in view of the highly significant regression of  $R$  on  $K_{max}$  and soil series. The table in appendix <sup>10,4,3</sup> shows that broadly this is so. However, the contrasting feature in the alternative approaches is the greater importance of  $K_{max}$  compared with the soil series in the analysis of variance. There may be three reasons. Firstly, the weighting caused by squaring the more serious deviations in the regression is not apparent in the analysis of variance since the  $K_{max}$  values are grouped and large deviations are hidden in the group means before squaring. Secondly, in the analysis of variance, the polynomials were selected in the order  $K_{max}$  (linear and quadratic) and then soil series. The latter contrast, in order to maintain orthogonality, involved only 8 out of 20 sites. Had priority been given to the soil series contrast then the result may have been different. Thirdly, the value  $R$  is a

kind of linear transformation eliminating the influence of the variation in the absolute magnitude of the seed/ware ratios at different sites discussed in detail in appendix <sup>10,4,3</sup> /. As suggested there the analysis of the transformed data is more meaningful than that of the raw data since differences due to the absolute values of the seed/ware ratios are extraneous to the model being tested.

So the choice lies between the alternative methods of transformation shown in fig. 3,2,4 and table 3,2,1. Both are linear transformations although the data in table 3,2,1 would benefit from log transformation as discussed in appendix <sup>10,4,3</sup> /. As suggested above the regression approach emphasises deviations of individual points whereas grouping tends to eliminate this weighting. The added advantage is that the rate and type of  $K^+$  and their interaction affects are more easily displayed since  $K_{\max}$  can be converted to a scale of soil  $K^+$  and the fertiliser  $K^+$  effect can use the same abscissa. This has been used to define the model.

### 3,2,5. Definition of the model

There are 2 effects to model, those of  $K_{\max}$  and soil series groups; it has been shown previously that their independent effects are substantial. The latter effect has been modelled in appendix <sup>10,4,4</sup> / but is emphasised less. This is not because it is less real but rather that being a complex of characteristics compared with  $K_{\max}$  it may be less easily understood.

The  $K_{\max}$  model must incorporate the following features reported in the relevant literature (see introduction):

1.  $K_{\max}$  is an exponential scale of soil  $K^+$ .
2. Soil  $K^+$  and fertiliser  $K^+$  both reduce the seed/ware ratio.
3. KCl produces a lower ratio where total available  $K^+$  is low and  $K_2SO_4$  the reverse.

These features are similar to those on which the model derived in section 3,1 was based. In fact the same model will suffice, with some signs reversed. Thus the standardised seed/ware ratio of a given rate of fertiliser  $K^+$  of a given type at a given value of  $K_{\max}$  of the group mean is

$$fX^{-1} [c - d(a + K_m^b) + e(a + K_m^b)^2 + A] - k' + k'' - t \pm tk' \pm tk'' + B$$

where  $f$  is a constant relating the absolute value of the group mean to that of a standard (note that this is a linear transformation and a log transformation would be better).

$X$  is a standard value (level 1 of KCl in this case but it could be any finite value),

$c$ ,  $d$  and  $e$  are respectively a constant and the linear and quadratic coefficients of the regression relating the group mean seed/ware ratio to soil  $K^+$  status,

$a$  and  $b$  are a constant and an exponent relating  $K_{\max}$  (the group mean is  $K_m$ ) to soil  $K^+$  status,

$k$ ,  $t$  and  $kt$  are the linear ( $k'$ ) and quadratic ( $k''$ ) effects of rate of  $K^+$ , and  $t$  the main effect of type of  $K^+$  and  $kt$  the interaction effects between them calculated within the data means of the  $K_{\max}$  groups,

$A$  and  $B$  are the error terms of the regression involving the constants  $c$ ,  $d$  and  $e$  and estimation of the effects  $k$ ,  $t$  and  $kt$  respectively.

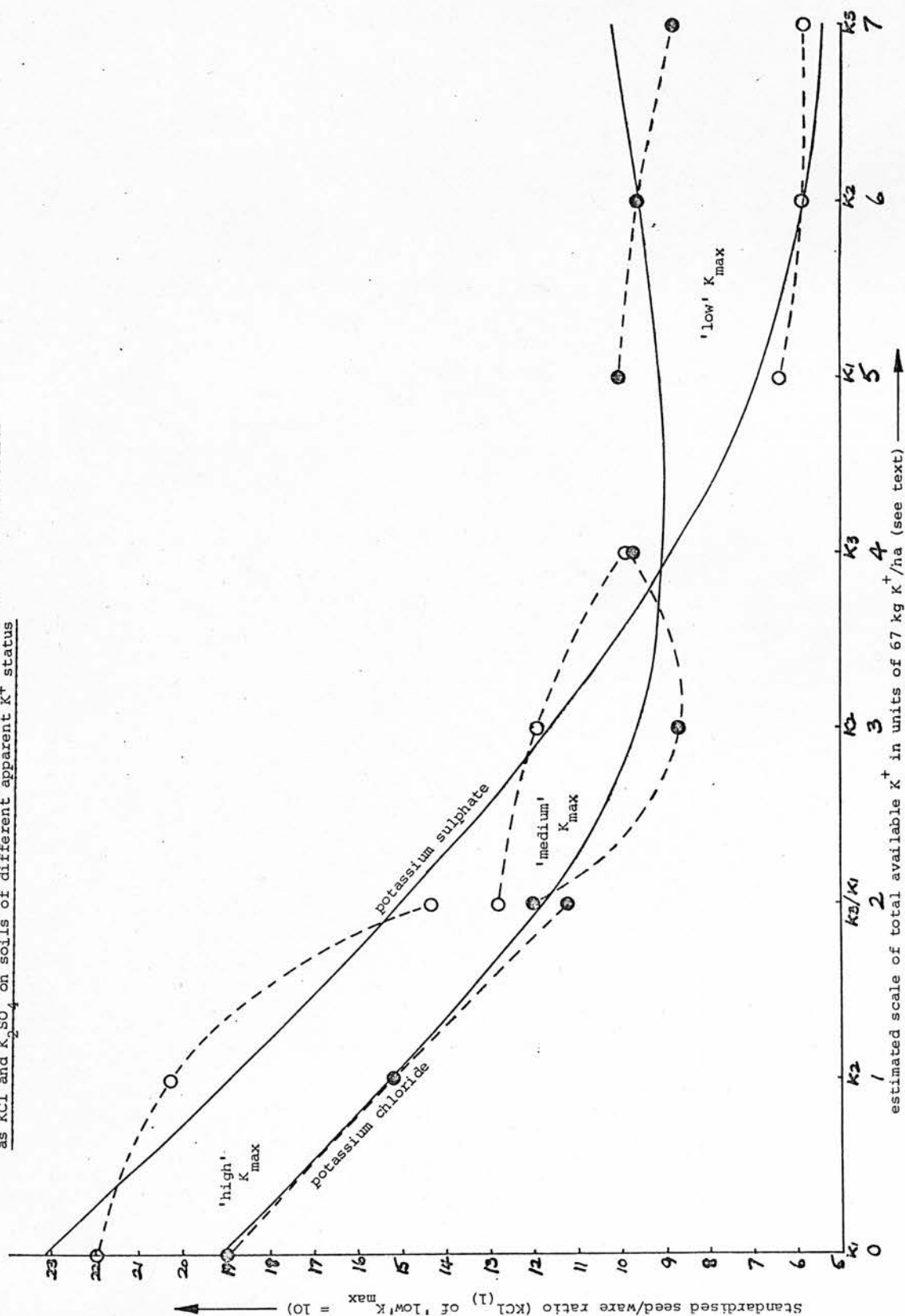
For each group  $k$ ,  $t$ ,  $kt$  and  $B$  can be calculated. Arbitrary values of  $a$ ,  $b$  and  $f$  can be inserted and the equation solved to estimate  $c$ ,  $d$ ,  $e$  and  $A$ . With systematic variation of constants  $a$ ,  $b$  and  $f$  within reasonable limits the minimum value of  $A$  can be found. If the values of  $a$ ,  $b$  and  $f$  are found at which the estimates of  $A$  for both  $KCl$  and  $K_2SO_4$  are minimum then the model could be said to have the best fit to the data. Thus although the use of constant  $f$ , which removes extraneous variation between the  $K_{max}$  groups, seems arbitrary, its value in reality is fixed by the relative positions of the 6 type  $x$  rate of  $K^+$  points in each  $K_{max}$  group. It was necessary to use  $f$  in this model unlike in that of total yield.

### 3,2,6. Proving the model

As stated in section 3,1 perfecting the model could be done by computer but in fig. 3,2,7 it has been fitted 'by eye'. As anticipated from the literature, the result is a pattern of 2 distinct curves formed by  $KCl$  and  $K_2SO_4$  which cross-over at an intermediate level of total available  $K^+$ . The origin of the abscissa is at an assumed level of soil  $K^+$  of 13 Kg/ha so that the interception occurs at a level of about 280 Kg/ha of total available  $K^+$ .

The constants  $a$  and  $b$  were those estimated in equation (2) in section 3,1 and they fixed the position of the  $K_{max}$  group means on the abscissa. The constant  $f$ , was 10 for the 'low'  $K_{max}$  group, 12 for 'medium' and 19 for 'high'. These fixed

FIG 3,2,7 Model of the effect on seed/ware ratio of potatoes of fertiliser  $K^+$  as  $KCl$  and  $K_2SO_4$  on soils of different apparent  $K^+$  status





the position of the  $K_{\max}$  group means on the ordinate. Using the 9 points on each curve, the regressions were

$$Y_{KCl} = 18,6 - 4,1K + 0,42K^2 \pm 1,08$$

$$Y_{K_2SO_4} = 22,9 - 4,9K + 0,35K^2 \pm 1,36$$

In themselves the standard errors are meaningless being dependent on the values of a, b and f and the transformation used. However, in the sense that they are inversely related near their minima they might be used to test the difference between the regression<sup>s</sup>. On this basis the regressions are significantly different at  $P = 0,001$ . As can be seen in appendix 9 when the absolute value (in this case seed/ware ratio) is high then a log transformation should reduce the difference between the treatments more than a linear transformation. Had a log transformation been used in this model then the KCl and  $K_2SO_4$  points in the 'low'  $K_{\max}$  group would have been closer and the model an even better fit.

For the reasons described in appendix <sup>10,4,2</sup> this exercise was completed on the ratio of the number and not weight of seed and ware tubers. As such the model cannot be used in an economic appraisal of its consequences.

### 3,2,7. Summary of section 3,2.

The relative effect on the seed/ware tuber number ratio of KCl and  $K_2SO_4$  was found to vary with the soil  $K^+$  status as measured by the magnitude of the response to  $K^+$ , and soil series the known contrasts of which were texture and drainage. The effect of estimated soil  $K^+$  status confirmed the model obtained

from reports of other trials and was related to the model of the effect of KCl and  $K_2SO_4$  on total yield derived in section 3,1. Both models demonstrated more perfect  $K^+$  nutrition from KCl than  $K_2SO_4$  on  $K^+$  deficient soils but the reverse on  $K^+$  sufficient soils. This effect was greater than predicted on sandy and freely drained soils but less on heavy and imperfectly drained soils.

### 3,3 GENERAL DISCUSSION OF SECTIONS 3,1 AND 3,2

Four questions arise.

1. To what extent is the value  $K_{max}$  a realistic measure of soil  $K^+$  status?
2. What is the explanation of the soil series effect after removal of the  $K_{max}$  effect?
3. What is the significance of the models relating total available  $K^+$  and the 2 fertiliser types to yield and seed/ware ratio?
4. Providing the link with succeeding sections, what is the mechanism of the effects?

The position of  $K_{max}$  normally encountered is as the dependent variate affected by soil  $K^+$  status. The simple relationship is too simplistic (Armitage and Groves, 1971) and most recent models to predict the level of a nutrient which maximises yield or net output involves the covariance of more factors than soil nutrient status (eg. Russell, 1968; Colwell and Esdaile, 1968; Greenwood et al, 1971). The concept of the 'availability' of the nutrient is one of an empirical procedure to extract and measure a proportion of the total

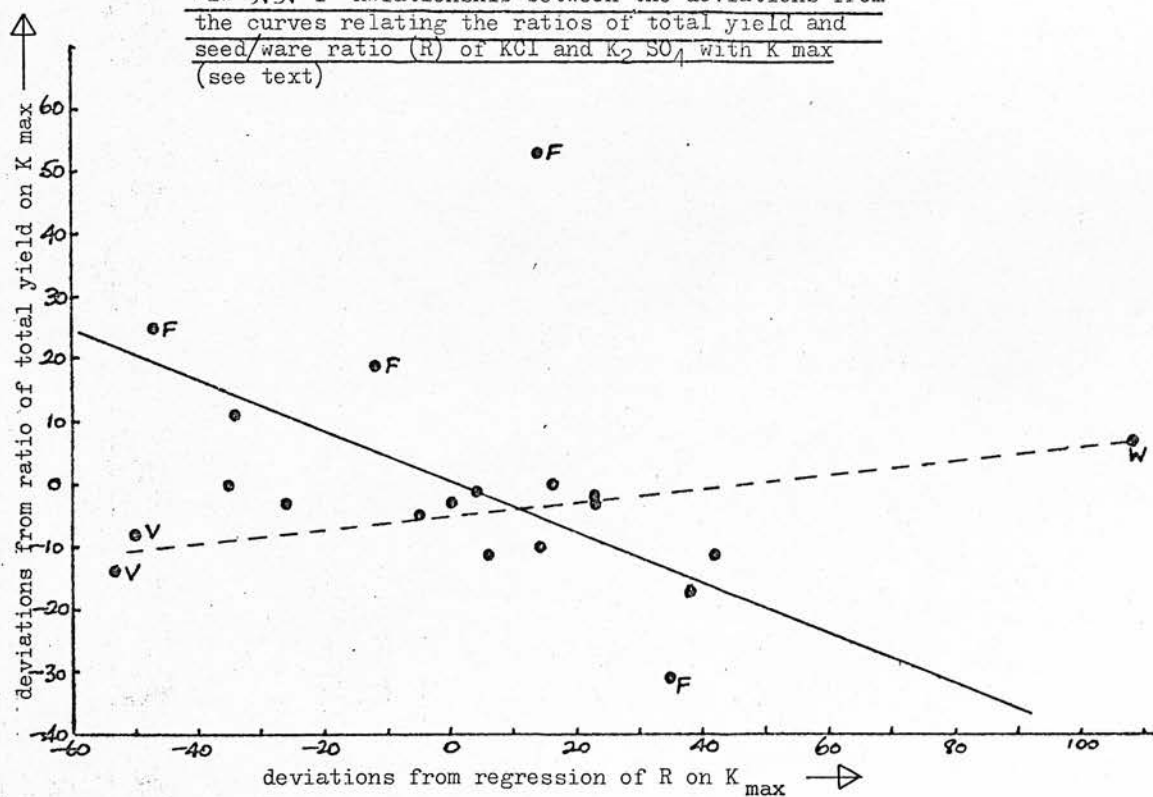
soil reserve, quantified by measures of other affecting variates. In this sense ~~an~~ empirically exchangeable  $K^+$  is no more a parameter of 'available'  $K^+$  than is  $K_{\max}$ . In this paper the use of  $K_{\max}$  as an index of available  $K^+$  is understood to be a complex of potentially available  $K^+$  the exploitation of which by the crop is limited by other factors. As such its relationship to empirically exchangeable soil  $K^+$  would not be linear. Furthermore the variation in the values of the unknown limiting factors to be expected from a nearly random selection of sites would be expected to produce scattering about the theoretical regression of exchangeable  $K^+$  on  $K_{\max}$ . This scatter should not change the general form but it has implications for any function fitted to a scale of exchangeable soil  $K^+$  estimated from a scale of  $K_{\max}$ . In the preceding sections 3,1 and 3,2 functions of yield and seed/ware ratio have indeed been fitted to such a scale. Despite the large random variation expected from the poor estimates of the functions, arising from the experimental design used, some systematic variation was identified, associated with soil series scored for a composite of increasingly heavy texture and impedance of drainage.

In fig. 3,1,3 a large positive deviation from the regression reflects in terms of total yield the tendency for KCl to provide relatively more perfect nutrition than  $K_2SO_4$  than the regression predicts, whether or not the effect is due to  $K^+$  or the anion or both. In section 3,2,4 it is argued that a large negative deviation of R from its regression on  $K_{\max}$  similarly reflects the superior nutrition of KCl. It follows then that deviation from figs. 3,1,3 and 3,2,4 should

be negatively correlated. Such a correlation clearly exists as shown in fig. 3,3,1. And from the discussion of these figs in sections 3,1 and 3,2 it may be generalised that KCl affords relatively more perfect nutrition than  $K_2SO_4$  on sandy, freely drained soils and the reverse on heavy imperfectly drained soils. However, of the 6 most obvious deviations from the regression in fig. 3,3,1, 5 are the sandy, freely drained soils, the 2 Vinny series sites and 3 of the 4 Forfar series sites. The only meaningful aspect of this observation in view of the deviation being both positive and negative, is the axis formed between the extremes of soil type, the 2 Vinny series at one end and the deviating heavy soil, a Winton series at the other. This axis is shown in fig. 3,3,1 by a dashed line. Little importance can be attached to a function based on 3 points although the report by Kämpfer and Zehler (1967) of the superiority of  $K_2SO_4$  over KCl being greater on sandy than on heavy soils may be relevant.

The fact that deviations from 2 regressions are correlated would be expected if the common variate, in this case  $K_{max}$ , was poorly estimated. This raises again the point made above about the implication of systematic deviations from the regression of exchangeable  $K^+$  on  $K_{max}$  which results from failure to adjust the simple model by important covariants. It may be then, that by a rather circuitous pathway the main covariant in the  $K_{max}$ : exch.  $K^+$  regression has been identified as the composite of soil texture and drainage.

FIG 3.3. 1 Relationship between the deviations from the curves relating the ratios of total yield and seed/ware ratio (R) of  $KCl$  and  $K_2SO_4$  with  $K_{max}$  (see text)





This simple explanation, however, is not the only one possible. The hypothesis advanced in section 3,2 proposes more perfect  $K^+$  nutrition from KCl than from  $K_2SO_4$ , manifesting its effect as a greater quantity of available  $K^+$ . If this hypothesis is correct it is difficult to explain why quantitatively the effect should be greater on sandy, freely drained soils. Uptake of  $K^+$  from KCl may be more rapid than from  $K_2SO_4$  and in a soil with a high leaching intensity this feature may lead to greater uptake from KCl. Terman et al (1953) suggested that the greater solubility of KCl was responsible for the greater uptake of  $K^+$  from this source but Harrap (1960) discounts this. However it may eliminate rate of  $K^+$  uptake as an explanation of the soil series effect since KCl would be more rapidly leached in a freely draining sandy soil.

Another explanation of the soil series effect stems from the observation that  $K_2SO_4$  provides relatively more perfect nutrition than KCl on heavy, imperfectly drained soils. The reason for the relatively poorer performance of KCl where  $K_{max}$  is low is discussed later but if the net effect is assumed to be a result of toxicity of  $Cl^-$  then KCl is proportionately more toxic on heavy soils with impeded drainage. The effect may be due to the greater retention of  $Cl^-$  in these soils although this was not measured. It is expected that this condition would be exacerbated by proximity to the sea. Site M4 was a Macmerry soil series about 200 m from the sea where KCl performed relatively much better than the model predicts. Sites F3 and F4 were Forfar soil series

about 6 and 7 km inland from the Angus coastline, at both of which  $K_2SO_4$  performed relatively much better than predicted. Six km is not far from the sea in terms of wind blown salt spray but few sites were further from the coast than this. Thus there is no evidence to support this explanation.

A third possible explanation is the converse of that given previously; heavy soils are deficient in S. The use of ammonium nitrate, triple superphosphate, ammoniated superphosphate and muriate of potash has considerably reduced the return of S to arable soils in recent years. However, although S levels at the experimental sites were not measured, S deficiency is unlikely and no symptoms were observed in the crops. F.Y.M. was applied to most sites which furthermore were downwind of mining areas in Fife and East Lothian some with continually burning spoil-heaps and the industrial axis of Scotland where S deficiency is unlikely to occur.

A fourth explanation may be that the potash types are interacting with a characteristic of the soils other than texture and drainage, which has not been specified or emphasised but none-the-less quantitatively orders the series in the same way. Obvious candidates are the many characteristics which often are correlated with texture such as pH, GEC, base saturation, exchangeable  $Ca^{2+}$  and  $Mg^{2+}$ , organic matter, bulk density, available moisture and permeability (Armitage, 1971). For example, Williams *et al.* (1958) demonstrated that the P-sorption capacity at pH 4 of soils derived from old red sandstone till is lower than that of soils derived from fine-grained sediments. This suggests

a scale of P-sorption capacity from Vinny to Winton series (although the evidence of mean available P content given in appendix 10,2 does not support this). Simpson and Crooks (1961) showed that  $K^+$  reduced the seed/ware ratio more at high rates of N and P than at low rates. If in a sandy soil the P-sorption capacity is lower and the proportion of fertiliser P which is unfixed by the soil is greater then  $K^+$  rate and type effects are measured at an effectively greater rate of P. However, for this to be true the mean response to P on the sandier soils must be greater but there is no evidence that this is so. Nor does it explain why the relative effects of KCl and  $K_2SO_4$  should be reversed. However, after the simple explanation given first, this type of effect may be the most satisfactory explanation of the effect of soil series on the source of potash effects on yield and size distribution. Indeed it may be complementary in the sense that the real covariants of the  $K_{max}$  on each  $K^+$  regression may include a factor such as those suggested above in addition to texture and drainage.

The deviations discussed above perhaps are difficult to explain. The grouping of sites to provide mean  $K_{max}$  values of the 3 clusters into which they tended to fall naturally does not ignore the existence of other affecting variates. Nor does it seem to weight the groups because  $K_{max}$  was almost independent of soil series. However, from the simplification emerged two important effects illustrated in figs. 3,1,5 and 3,2,7. The fact that the two models of yield and size distribution are so similar is real evidence that as far as

K rate and type are concerned the features are related by a common mechanism. Indeed, it appears that the relatively greater production of large tubers by either KCl or  $K_2SO_4$  results in a greater total yield. This is parallel to the observation that yield response to  $K^+$  is accompanied by an increase in the proportion of large tubers. The syndrome has been described earlier as 'more perfect  $K^+$  nutrition'.

The second feature of these models is the tendency of KCl to be the superior source of  $K^+$  on  $K^+$  deficient soils and  $K_2SO_4$  the superior on  $K^+$  sufficient soils. The economic implications of this fact are the subject of section 3,4. The reality of this statement insofar as it described the data for 1 series of trials in S.E. Scotland is independent of the 'loss' of difficult-to-explain deviations in the  $K_{max}$  groups, of the accuracy of the equivalence of  $K_{max}$  and soil  $K^+$  scales and of the subjectiveness of compensating the seed/ware ratios for extraneous effects. The superiority of KCl on  $K^+$  deficient soils was a highly significant effect even in the untransformed data. Furthermore, the 'cross-over' points of the KCl and  $K_2SO_4$  regression lines on total available  $K^+$  were 250 kg K/ha for yield and 280 kg K/ha for seed/ware ratio. This difference is very small considering that the regressions were aligned and drawn by eye but independently of each other. The data of Simpson and Crooks (1965) suggested a 'cross-over' point at a rate of fertiliser of 298 kg K/ha (see section 3,2,1), but this must be added to the mean soil  $K^+$  status, at least 150 kg/ha. Clearly the soil series chosen for the trials will cause a weighting and a shift in this cross-over point as may season and husbandry too. Therefore the

equivalence point of KCl and  $K_2SO_4$  has no fundamental value in terms of total available  $K^+$ . It may be for this reason that although the effect has been reported in several papers (eg. Dickins et al. 1962; Gething, 1968) nowhere has it been claimed as a fundamental property.

On a  $K^+$  deficient soil, fertiliser  $K^+$  may be expected to increase the proportion of large tubers and thereby increase total yield. At a common but low soil  $K^+$  status, KCl produces a greater proportion of large tubers and total yield than an equivalent but moderate rate of  $K_2SO_4$ . In this context 'more perfect  $K^+$  nutrition' may mean either simply 'more available  $K^+$ ' from KCl than from  $K_2SO_4$  or a synergistic effect of  $K^+$  and  $Cl^-$  on the biochemistry and growth. A more abstruse explanation may attempt to relate synergism of  $Cl^-$  (or  $K^+$  and  $Cl^-$  together) with a feature of the soil environment which is correlated with low  $K^+$  status. Furthermore, for completeness, since the effect is relative it may be the antagonistic effect of  $SO_4^{2-}$  (or  $K^+$  and  $SO_4^{2-}$  together) at low soil  $K^+$  status or a correlated factor, or in simple terms an 'imbalance' of  $K^+$  and  $SO_4^{2-}$ , which is responsible.

The same format of explanation applies in the opposite situation where at high soil  $K^+$  status, a heavy rate of  $K_2SO_4$  produces relatively larger tubers, and hence yield, than the equivalent rate of KCl. Here it is important to distinguish between the osmotic consequence of high salt concentration as reported by Simpson (1963) for example and as seen at the highest rates of both sources of  $K^+$  in fig. 3,1,5, and the relative effect of the 2 sources. There is little reason to



predict the greater osmotic effect of KCl than an equivalent rate of  $K_2SO_4$ ; both salts are relatively soluble but KCl may be leached more rapidly than  $K_2SO_4$ .

### 3,4,1 The economic consequences of the model

With seed potatoes selling at considerably higher prices than ware it is clear that if the seed/ware ratio is influenced by rate and type of fertiliser  $K^+$  and soil  $K^+$  status the economic optimal level of K will be affected also. Holmes *et al* (1973) fitted the regression  $y = a + b x + c x^2$  to the seed and ware yield response curves to K reported by Dickins *et al* (1962) and Birch *et al* (1967). Optimising the 'profit' (net output) curve they showed that  $K_2SO_4$  is more economic for seed production than KCl but that the optimum rate of  $K_2SO_4$  for seed production should be about 10% less than that recommended for the ware crop. In one series of trials, KCl was more profitable than  $K_2SO_4$  at low rates of application; the 'cross-over' occurred at about 100 kg of  $K^+$ /ha.

Appendix 10,4,5 describes the derivation of the equation which calculates the level of K for maximising net output in this series. The equation  $y = ax + bx^2$  was fitted and the lowest level of fertiliser  $K^+$  was 101 kg/ha and the interval 67 kg/ha. Using the current value of seed as £30 per tonne and ware £22 per tonne and the current cost of  $K^+$  as KCl at £0,1336 per kg (of  $K^+$ ) and as  $K_2SO_4$  at £0,2185 per kg the resulting equations (eqns (8) and (9) in appendix 11) the  $K^+$  required to maximise gross output is

$$K_{KCl} = 67 \left( \frac{4,54 - v_w a_w - v_s a_s}{2(v_w b_w + v_s b_s) - 8,95} \right) + 34$$

$$K_{K_2SO_4} = 67 \left( \frac{7,43 - v_w a_w - v_s a_s}{2(v_w b_w + v_s b_s) - 14,64} \right) + 34$$

The level of fertiliser  $K^+$  which maximises yield is dependent upon the absolute value of mean yield (Holliday, 1963); this must apply equally to the seed and ware components of total yield. Appendix / <sup>10,4,5</sup> shows the  $K_{max}$  group mean yields of seed and ware for each rate and type of fertiliser  $K^+$  weighted by the mean total yield. The values of the calculated coefficients and the optimum level of fertiliser  $K^+$  are shown in table 3,4,1 below. The level of soil  $K^+$  equivalent to the mean  $K_{max}$  value was estimated by the approximation:

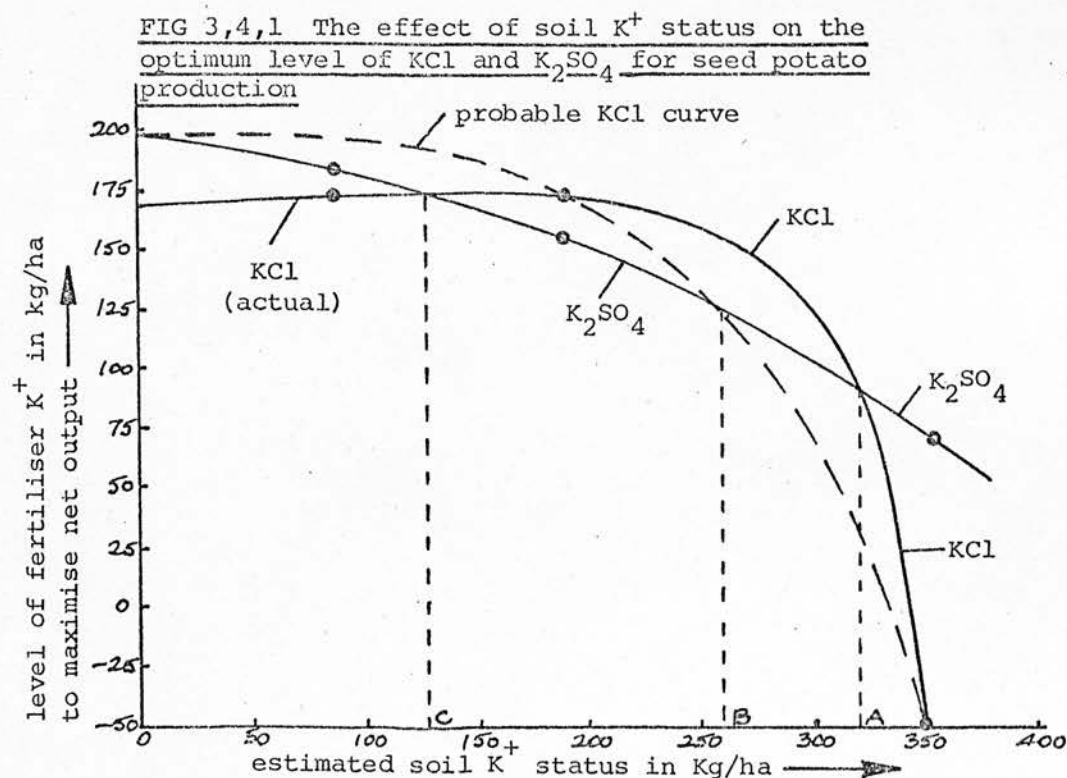
$$K_{soil} = 2323 - K_{max}^{941} \text{ (eqn. (2), section 3,1)}$$

Table 3,4,1: The optimum rate of fertiliser  $K^+$  on soils of different K status

| $K_{max}$<br>group mean | equivalent<br>$K^+$ soil<br>in kg/ha | Type<br>of<br>$K^+$ | crop<br>fraction | coeffs.<br>a b | opt.fert. $K^+$<br>kg/ha |
|-------------------------|--------------------------------------|---------------------|------------------|----------------|--------------------------|
| 'low' 125               | 350                                  | KCl                 | W                | -1,15 0,28     | -51                      |
|                         |                                      |                     | S                | 2,05 -0,59     |                          |
|                         |                                      | $K_2SO_4$           | W                | 2,82 -0,74     | 71                       |
|                         |                                      |                     | S                | -0,96 -0,23    |                          |
| 'medium' 184            | 192                                  | KCl                 | W                | 2,65 -0,45     | 174                      |
|                         |                                      |                     | S                | 4,83 -1,10     |                          |
|                         |                                      | $K_2SO_4$           | W                | 2,16 -0,54     | 154                      |
|                         |                                      |                     | S                | 4,56 -1,00     |                          |
| 'high' 242              | 80                                   | KCl                 | W                | -0,79 0,17     | 172*                     |
|                         |                                      |                     | S                | 3,26 -0,59     |                          |
|                         |                                      | $K_2SO_4$           | W                | 0,39 0,16      | 184                      |
|                         |                                      |                     | S                | 5,96 -1,21     |                          |

\* Note: this value is suspect being derived from the mean of only 2 sites; KCl decreased ware where the reverse was expected.

The optima shown in table 3,4,1 are plotted against estimated soil  $K^+$  status in fig. 3,4,1



Extrapolating the  $K_2SO_4$  curve back to the ordinate suggests the greatest amount of  $K^+$  that need be applied to seed potatoes even on the most deficient soils is 200 kg/ha of  $K^+$ . At this point according to the models discussed previously the source of fertiliser is immaterial; the curves of both types have a common origin. This justifies the assumption that the real estimate of the optimal level of  $K^+$  as KCl in the 'high'  $K_{max}$  group is incorrect. The dashed line in fig. 3,4,1 shows the expected regression of KCl on soil  $K^+$  status. The actual KCl line cuts the  $K_2SO_4$  line twice at levels of soil  $K^+$  approximately A and C. However, this situation is not

likely to occur and the probable KCl curve intercepts the  $K_2SO_4$  curve once only at a soil  $K^+$  status of about 260 kg  $K^+$ /ha (point B). By using the data from 20 trials from a single season and more recent economic values, the conclusion of Holmes *et al.* (1973) that  $K_2SO_4$  is the economically superior source of  $K^+$  for seed potatoes, seems only to apply when the soil  $K^+$  status is above about 260 kg/ha of available  $K^+$ . Below this  $K^+$  status then KCl is the superior source, at least in S.E. Scotland where much of the arable land is indeed below this level.

The cross-over in fig. 3,4,1 occurs at a theoretical total available  $K^+$  status of  $260 + 125 = 385$  kg  $K^+$ /ha. This is considerably greater than the cross-over points, in terms of available  $K^+$ , in the models of total yield and seed ware ratio described earlier in which the values were 250 and 280 kg  $K^+$ /ha respectively. This discrepancy reflects the weighting caused by the use of seed/ware ratio on a tuber weight rather than number basis and by the greater value of the seed fraction and the greater unit cost of  $K_2SO_4$ .

The independent effect of soil series should be recalled since that too will affect the conclusion. It was found that on the sandy and freely drained soils derived from old red-sandstone till the seed/ware ratio was lower and the total yield greater from KCl than the models predicted. This implied that the extra yield came from more ware tubers and total value would be increased. Therefore, generalising about the effect of soil series it may be concluded that the level of soil  $K^+$  at which  $K_2SO_4$  becomes the superior source

of  $K^+$  for seed production would be greater than 260 kg/ha on sandy freely drained soils but less than 260 kg/ha on heavy and imperfectly drained soils, assuming that texture and drainage were the determining characteristics of the 5 soil series involved.

### 3.5 SUMMARY OF CHAPTER 3

Some of the data from 25 routine potato manurial trials in S.E. Scotland in 1966 have been examined in detail. A pattern has emerged which suggests firstly that any tendency of KCl or  $K_2SO_4$  to produce relatively more large tubers than the other source will result in a greater total yield and secondly that KCl produces more perfect  $K^+$  nutrition on  $K^+$  deficient soils and the reverse on  $K^+$  sufficient soils. These effects are relatively greater on sandy, freely drained soils and less on heavy soils with imperfect drainage. The soil series effect may be the main covariant expected in the regression of the level of fertiliser K required to maximise yield ( $K_{max}$ ) on soil exchangeable  $K^+$  status.

The economic significance of the models in 3.1 and 3.2 to potato seed production was estimated. On  $K^+$  deficient soils KCl is the superior source but on  $K^+$  fertile soils  $K_2SO_4$  is the superior source. The threshold on average was a soil  $K^+$  status of about 260 kg/ha of available  $K^+$  but it would be greater on sandy, freely drained soils and less on heavy, imperfectly drained soils.

It is required to explain the nature of the syndrome described as 'more perfect K nutrition' from KCl or  $K^+$



deficient and  $K_2SO_4$  on  $K^+$  sufficient soils. To do so it is necessary to

- 1, distinguish between the effects of  $K^+$ ,  $Cl^-$  and  $SO_4^{2-}$  together and individually,
- 2, assess their rates of uptake in relation to soil  $K^+$  status,
- 3, deduce the effect of differential uptake on the bio-chemistry and thence growth and development of the potato.

#### 4. SOIL OR PLANT ; CATION, ANION OR SALT EFFECT?

##### 4,1. INTRODUCTION.

The answer to the question of the relative effects of the fertilisers  $KCl$  and  $K_2SO_4$  on potatoes may be sought at different points on the scale of increasingly intensive study ranging from agronomy to sub-atomic structure. Two points on this scale are adopted in succeeding chapters, growth and chemical analysis. A problem which besets any study of this kind, however, is that whatever level of investigation is adopted it is almost impossible to discriminate between cause and effect. Recourse to the theory of probability contributes little. The reason is that a biological system is a dynamic equilibrium between a multitude of interacting processes. Even if this equilibrium can be reproduced experimentally any measurements performed on it are of a static state. The equilibrium is shifted experimentally and an attempt is made to interpolate data and make deductions about the dynamics of the system. But changing even a single component of the equilibrium sets off a multitude of chain reactions not one of which can be identified as causing the ultimate expression of the change. As Handley and Overstreet (1955) concluded, the effect of a specific ion cannot be ascribed to an individual metabolic process but rather to the sum total of its varied effects upon metabolism. Pragmatists argue that to identify the effect of a treatment in terms of the probability of its occurrence is adequate and to delve deeper is both wasteful and futile. This study as usual is a compromise. Before the results of growth and chemical

analysis are examined 2 fundamental questions require to be answered; is the origin of the treatment effect to be found in the soil or the plant and is it due to the cation, the anion or the interaction of them both?

#### 4.2. IS THE ORIGIN OF THE EFFECT IN THE SOIL OR THE PLANT?

The water solubility of KCl is greater than  $K_2SO_4$ , 310 and 90 g L<sup>-1</sup> respectively at 10°C. Could the differential effects of KCl and  $K_2SO_4$  originate in the difference of solubility? An extreme condition would be  $K_2SO_4$  applied in a band to a sandy textured soil at wilting point. (Scottish soils are rarely sands and rarely drop below wilting point). Supposing the water content of such a soil is 0,10g g<sup>-1</sup> and its apparent density is 1,7g cm<sup>-3</sup> and that the fertiliser is in contact with a cylinder of soil of cross sectional area 100 cm<sup>2</sup>, then the soil water in this band at 10°C would dissolve 6850 Kg/ha of KCl and 1990 Kg/ha of  $K_2SO_4$ . This is greater than would be applied in practice and it is unlikely therefore that the relative effects of these 2 fertilisers originate in their relative water solubility as suggested by Terman et al. (1953).

Because of the immobility of K<sup>+</sup> in the soil Cooke (1967) states that only about 5% of the K<sup>+</sup> required by a crop reaches the roots by mass flow. Contact absorption likewise is a small proportion leaving diffusion the main source of flux. At a concentration of 0,01 M and temperature 15°C, the diffusion coefficients of KCl and  $K_2SO_4$  are 1,4 and 0,9 cm<sup>2</sup> sec<sup>-1</sup> respectively in aqueous solution (International Critical Tables). Even though diffusion is slower in soil solution

(McGraw-Hill Encyclopedia of Science and Technology) it is expected that more  $K^+$  would be delivered to the roots from an application of KCl than  $K_2SO_4$ . Fixation of  $K^+$  from  $K_2SO_4$  may be greater due to its retention as a  $Ca K SO_4$  complex (MacIntyre et al. 1954).

Additional effects which have been noted are the increase in exchangeable  $Ca^{2+}$  and  $Mg^{2+}$  due to KCl compared with  $K_2SO_4$  (Wilcox, 1961) and the tendency for  $K_2SO_4$  to depress soil pH to a greater extent than KCl (Hanneman, 1964). If the former is true then a lower  $K^+$  absorption from KCl would be expected from the reduced free energy difference  $\Delta \bar{G}_{CaK}$  (Arnold, 1962). If an appreciable Donnan equilibrium exists in the soil for example with organic matter, other than with the roots then stoichiometrically more  $SO_4^{2-}$  would exist in soil solution than  $Cl^-$ .

Since both salts are almost completely dissociated at the concentration and pH in soil solution it is difficult to postulate any other mechanism in the soil to which could be attributed the observed differential effects of KCl and  $K_2SO_4$  as fertilisers for potatoes. Alternatively there is a plethora of evidence in support of differential uptake of  $K^+$ ,  $Cl^-$  and  $SO_4^{2-}$  from solution and physiological effects which result. It is for these reasons that the study developed towards a more detailed examination of growth and chemical composition in the hope of identifying a physiological mechanism within the crop as the main origin of the effect.

#### 4,3. IS THE EFFECT DUE TO THE CATIONS, ANIONS OR THE SALT?

In recent years there has been a rapid increase in understanding of the mechanism of ionic absorption and transport by plant tissue. There are several conceptual differences which have not been resolved yet but generally these are not relevant to this study.

##### 4,3,1. Ionic pathways

There is general agreement that the initial process of ion absorption is the diffusion of ions through the root epidermis into the cortex where a transitory Donnan equilibrium may be established (for example, Jacobson et al., 1958; Russell, 1963; Shone, 1967; Hiatt, 1967b; Epstein, 1973). In this phase the ratio of salt cations and anions is dependent upon the concentration of colloids and the electrostatic charge which they bear, the ratio of divalent to monovalent ions and upon the concentration of soil solution. The site of active ion absorption is the endodermis and the point of departure of the hypotheses of the leading experimentalists. What is clear is that the ion having entered the cytoplasm via the plasmalemma may be delivered by the tonoplast into the vacuole or be transported through the symplast eventually to be delivered into the xylem and distributed in the transpiration stream. Most theories postulate a carrier mechanism but over the kinetics of its function, its nature and its location there is considerable disagreement.



#### 4,3,2. Dual Isotherms

In 1952 Epstein and Hagan realised that a kinetic similarity may exist between the velocity of enzyme mediated reactions and carrier mediated ion absorption. Using roots in dilute salt solution they confirmed that the velocity of ion absorption could be predicted by a simple Michaelis-Menton equation. When the precision of the technique was improved and a wider range of solution concentration employed the absorption curve which hitherto had been considered simple emerged as a complex sequence of hyperbolic curves. Epstein and coworkers and many other experimentalists realised that by plotting the reciprocals of rate of absorption and solution concentration (Linweaver - Burke plot) that the first phase at lowest concentration may differ from subsequent phases in both slope and intercept. Accordingly Epstein ascribed fundamental significance to this difference defining a discrete mechanism ( system 1) at low concentration and another at high concentration (system 2). This pattern was found to occur in the absorption isotherms of several ions and the threshold generally was in the region 0,1 to 1 mM. Conjecture and disagreement developed over the siting of these mechanisms, variously at the plasmalemma, tonoplast or both. Tromp (1962) found that because from low concentration in the medium, absorption rate increases exponentially with increasing concentration to become independent at high concentration then only system 1 obeys the Michaelis-Menton law. System 1 has been associated with the filling of the cytoplasm (Osmond and Laties, 1967) and the absorption of ions by combination with

organic components up to the limit of their availability in the cytoplasm (Hiatt, 1968). Several authors agree that system 2 absorption is by diffusion and subject to Donnan phenomena.

The debate assumed a further dimension in 1971 when Nissen described the multiphase isotherm of  $\text{SO}_4^{2-}$  uptake. Claiming improved precision Nissen concluded that the data were best described by a single multiphase isotherm. Previously Pitman (1967) had suggested that dual isotherms may be an artefact of low salt status roots. In a reexamination of all comparable published data Nissen (1974) concludes that there is no evidence of the existence of 2 discrete absorption mechanisms. In a single system the carrier would need to undergo transformation at certain critical salt concentrations. In a review, Epstein (1973) does not agree and persists in recognising dual isotherms.

The debate is not vital to the interpretation of the results presented in this study. The important aspects of the theories of ion absorption are that the characteristics change as the concentration of the solution increases. Whether or not the mechanism undergoes a fundamental change of type or not is irrelevant.

#### 4,3,3. Cation and anion absorption

If indeed system 1 absorption operates over the whole concentration range and concurrently with system 2 absorption above a certain threshold then the latter, probably normal

diffusion, becomes proportionately more important as the concentration in the medium increases. Thus absorption at high concentration will be subject to Donnan phenomena (Hiatt, 1968) and absorption will be affected by root CEC and ratio of mono and divalent ions (Huffaker and Wallace, 1958). The relative number of -ve and +ve charges within the cytoplasm varies with species (Smith and Wallace, 1956; Hiatt, 1968) but the CEC of dicots is greater than monocots (Cunningham, 1964 III). Cunningham and Nielsen (1963) showed that the relative absorption of monovalent and divalent cations was unrelated to root CEC but that at high temperature and with a high rate of  $\text{NO}_3\text{-N}$  a monocot will behave like a dicot and absorb more divalent cations than monovalent. In a Donnan equilibrium relatively more monovalent ions diffuse into the cell than divalent (Elgabaly, 1962; Hiatt 1968). Overlapping of the root double layer of charge with that of a soil particle may suppress the CEC at least at the root surface, and increase the absorption of anions (Elgabaly and Wiklander, 1962). Increased absorption of anions is said to suppress the cytoplasmic -ve potential and cause an exponential increase in anion absorption (Macdonald and Laties, 1964; Torii and Laties, 1966b).

Several authors have noted the increase in respiration as the salt concentration of the medium increases but it is unlikely that respiration is the controlling mechanism of ion absorption (Handley and Overstreet, 1955) because the energy required for absorption is only a small fraction of that converted (Robertson, 1941). However, absorption is

related to the amount of sugar in the roots (Humphries, 1951).

The pH of the medium is well known to influence ion absorption; for example, at pH 4 the rate of absorption of P is related to the rate of transpiration becoming maximum at 6,0 (Hendrix, 1967), at which pH absorption is wholly as  $\text{H}_2\text{PO}_4^-$ . (Dijkshoorn, 1963). Maximum absorption rate of  $\text{SO}_4^{2-}$  is said to occur at pH 6,5 by Hendrix (1967) and pH 4,0 by Leggett and Epstein (1955). The effect of pH of the medium is reported to be greater on  $\text{K}^+$  than  $\text{Ca}^{2+}$  absorption (Dejaegere, 1966). At normal pH, Si may not be absorbed as an ion (McKeague and Cline, 1963) or may exist as a polymer of the weak acid  $\text{H}_2\text{SiO}_3$  (Dijkshoorn, 1962) and may enter as  $\text{SiO}_3^{2-}$  only above pH 9 (Dijkshoorn, 1963).

The maximum rate of ion absorption varies with the type and age of tissue and is inversely related to the salt concentration of the roots (Humphries, 1951; Pitman, 1969). It is clear from many published data that at low concentration the rate of  $\text{K}^+$  absorption from KCl is the same as that from  $\text{K}_2\text{SO}_4$  solution. Beyond the threshold of Epstein's systems 1 and 2 the rate of absorption of  $\text{K}^+$  from  $\text{K}_2\text{SO}_4$  hardly increases further whereas that from KCl increases exponentially (for example, Terman et al, 1953; Udovenko et al, 1964; Lüttge and Laties, 1966; Torii and Laties, 1966b). The absorption isotherms obtained by Hiatt (1968) are drawn in fig. 4,3,1:

Effect of solution concentration on ions absorption by excised  
barley roots (from Hiatt, 1968)

Fig. 4,3,1: On the absorption  
of  $K^+$  from KCl and  $K_2SO_4$

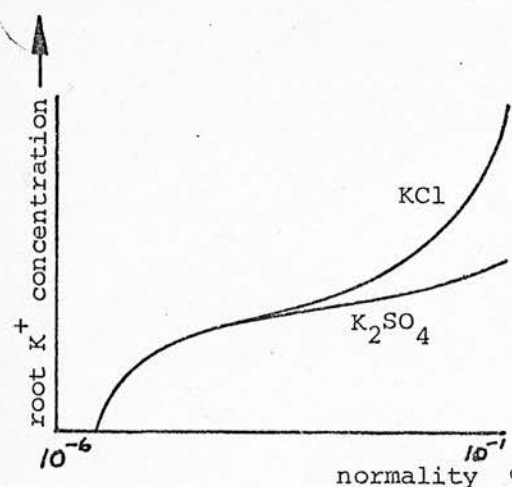
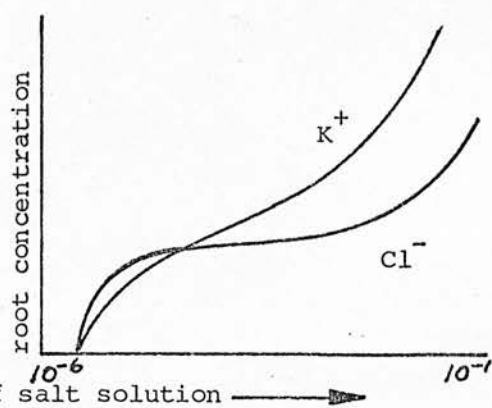


Fig. 4,3,2: On the absorption  
of  $K^+$  and  $Cl^-$  from KCl



The significance of this fact is that in the high concentration range the equilibrium tissue concentration of  $K^+$  should reflect the rate of absorption of  $K^+$  from the 2 salts because it is largely dependent upon the rate of absorption and independent of the concentration of the external solution (Osmond and laties, 1968; Pitman, 1969). Because rate of absorption is dependent upon the solution concentration then it is to be expected that the equilibrium concentration of  $K^+$  and  $Cl^-$  should be reached more rapidly at high concentration (Hiatt, 1968). However, as Hiatt noted, the difference in equilibrium concentration was less than the concentration found after only 4 hours. The threshold of systems 1 and 2, or between the first 2 phases, in this case was about 0,5 me/L. Fig. 4,3,2 shows that at the same concentration the isotherms of  $K^+$  and  $Cl^-$  absorbed from KCl solution intercept; above about 0,5 me/L of KCl the absorption of  $K^+$  is greater than  $Cl^-$ . Hiatt suggests the



isotherms become parallel and the differences within the range tested was absolute. Pitman (1969) estimated the difference as about 10%.

From  $K_2SO_4$  solution the absorption pattern is less clear because the absorption of  $SO_4^{2-}$  after 4 hours is negligible; there is evidence that the  $K^+$  and  $SO_4^{2-}$  isotherms never intercept and  $CaCl_2$  and  $K_2SO_4$  hardly show system 2 absorption (Hiatt, 1967b and 1968). Handley and Overstreet (1955) define  $K^+$ ,  $Na^+$ ,  $NO_3^-$ ,  $Cl^-$  and  $HCO_3^-$  as rapidly absorbed ions which stimulate salt respiration and  $Ca^{2+}$ ,  $Mg^{2+}$  and  $SO_4^{2-}$  as slowly absorbed ions which have no effect on respiration. Udovenko et al (1964) rate the counter anions in decreasing order of rate of  $K^+$  absorption as  $HCO_3^-$ ,  $Cl^-$ ,  $H_2PO_4^-$ ,  $NO_3^-$  and  $SO_4^{2-}$  and the absorption of  $K^+$  and  $Na^+$  is greater in the presence of  $Ca(HCO_3)_2$  than  $CaSO_4$  (Naumann, 1966). Rains and Epstein (1967) observed that  $Na^+$  absorption is less influenced by the anion than  $K^+$ . The influence of the cation upon the rate of absorption of the anion displays the same effect of valency as in the absorption of cations. Thus  $Cl^-$  shows dual absorption isotherms with rate within the range of system 1 unaffected by the cation, but above the threshold  $K^+$  greatly stimulates rate of absorption compared with  $Ca^{2+}$  (Lüttge and Laties, 1966). Hiatt (1968) proposed that in this situation, absorption of  $Cl^-$  from  $CaCl_2$  proceeds at the same rate as from  $KCl$  only as long as endogenous organic salts of  $K^+$  are available for decarboxylation to utilise the  $H^+$  absorbed along with  $Cl^-$ . Once the cytoplasm has been depleted, the rate of  $Cl^-$  absorption from  $CaCl_2$  drops markedly.

Although  $K^+$  can be absorbed from pure bentonite, presumably by exchange for  $H^+$  (Handley and Overstreet, 1955), many authors consider that the control of cation absorption is the absorption of anions (Dijkshoorn 1967; Cunningham, 1964II; Pitman *et al.*, 1968). Easily absorbed ions may enter the cytoplasm as ion pairs, for example  $KCl$  and  $KNO_3$  (Cunningham and Nielsen, 1965 V; Hiatt, 1968) but generally the absorption pattern is too complex for this to be a controlling mechanism. There is strong evidence, however, that at least part of the control resides in the ability of the tissue to synthesise organic acids (for example de Wit *et al.*, 1963; Hiatt, 1968; Jacoby and Laties, 1971) although in recent reviews Nissen (1974) tends to reject this idea and Epstein (1973) ignores it.

#### 4,3,4. Differential absorption of cations and anions and the role of organic anions.

The theory that a constant relationship existed for any plant species between the stoichiometric total of cations and anions was advanced by Walker (1945) and formalised by Bear (1950). The ability of 1 cation to replace another without greatly affecting the stoichiometric total had been recognised earlier (for example von Italic, 1938). Dijkshoorn (1957 a and b) found that with increasing  $NO_3-N$ , cation absorption is increased and that because  $Ca^{2+}$  and  $Mg^{2+}$  were only slowly absorbed by ryegrass, the increase was mainly  $K^+$  and  $Na^+$  even though  $Ca(NO_3)_2$  and  $Mg(NO_3)_2$  were applied. As evidence accumulated that the sum of cations was not constant and that ions can substitute for one another so the ratio theory emerged.

Bear (1950) concluded that any plant tissue has a maximum capacity for cations and that imposes a limit too on anion absorption. Dijkshoorn (1957b) found that ryegrass has a maximum capacity for cations of about 200 me/100g of dry matter. Fertiliser with  $\text{Cl}^-$  as the dominant anion caused the uptake of cations to increase and although P and S absorption were diminished,  $\text{Cl}^-$  more than compensated and total inorganic anions increased too (Dijkshoorn and Hart, 1957). Although many authors (quoted by Cunningham, 1964 II) considered the ratio rule to be fundamental to a species at given pH, it became clear that it was related in some way to, or even controlled by N metabolism and more especially by the absorption of N as  $\text{NH}_4^+$  or  $\text{NO}_3^-$  (Dijkshoorn, 1959b and 1958; Cunningham, 1964 I and II; Cunningham and Nielsen, 1965V). The ratio was found to vary with age (Said, 1959) and with supply of  $\text{Na}^+$  and  $\text{Cl}^-$  but not  $\text{K}^+$  (Cunningham 1964 II) although Dijkshoorn (1957a) had found it independent of the type of cation accompanying a constant rate of  $\text{NO}_3\text{-N}$ . However, the significance of the influence of N metabolism on the ratio and indeed the effect of different combinations of rapidly and slowly absorbed ions upon control of ion absorption and growth seems to have emerged more recently.

Absorption of cations generally is thought to occur in exchange for  $\text{H}^+$  or  $\text{K}^+$  with the medium (Burstrom, 1945; Jacobson and Ordin 1954; de Wit et al, 1963; Cunningham and Nielsen, 1965V; Torii and Laties, 1966a; Hiatt, 1968), and anions  $\text{OH}^-$  or  $\text{HCO}_3^-$  (Walker, 1960; Dijkshoorn, 1962; Jacoby and Laties, 1971). The change in pH of the medium resulting from salt absorption clearly is dependent upon the relative rates

of cation and anion absorption (Jacobson and Adams, 1963; Hiatt, 1967b) although in soil the change is buffered by desorption of  $H^+$  from the exchange complex (Walker, 1960). With a change in medium pH, there is an equivalent but opposite change in the pH of the cell sap (Mulder, 1948; Kirkby and Mengel, 1967; Hiatt 1967a and b). With a marked change in tissue pH growth is reduced (Dijkshoorn, 1962).

Only in exceptional cases, notably with KCl, is the absorption of cations and anions stoichiometrically equal (Pitman et al, 1968; Hiatt, 1967b). The stoichiometric balance in the tissue of cations over inorganic anions was first realised to be provided by organic anions by Böning and Böning-Seubert in 1932 and verified by Ulrich in 1941. The absorption of anions, at least when N is absorbed as  $NO_3^-$  is always greater than cations, termed acidic uptake because of the nominal absorption of  $H^+$  but the metabolism of N and S releases  $OH^-$  or  $HCO_3^-$  which is excreted or converted into organic anions to balance the surplus of cations over the remaining inorganic anions (Van Tuil, 1965). Thus as in studies on cation/anion ratio, N metabolism is intimately linked with organic acid synthesis. Clearly it is the comparison of the effects of fertilisation by  $NH_4-N$  which demonstrates most effectively this involvement. The latter is well known to stimulate organic acid synthesis (Kirkby and Mengel, 1967; Jacoby and Laties, 1971) although Joy (1964) attributed the effect of  $NH_4-N$  to the increased absorption of P. Dijkshoorn (1963) observed that excess  $NH_4-N$  and N deficiency, including the gradual exhaustion of  $NO_3^-$  in the medium, cause the organic acid concentration to fall. The

organic anion concentration is greatest in leaves partly due to the retention of  $\text{Ca}^{2+}$  and  $\text{Mg}^{2+}$  as immobile organic salts and partly to the reduction of  $\text{NO}_3^-$  (by the reductase system normally located there in non-legumes (Wallace and Pate, 1967)) which balanced the  $\text{Ca}^{2+}$  and  $\text{Mg}^{2+}$  in transport from the roots (Kirkby and Mengel, 1967).

Nitrogen treatment is not alone in influencing the organic acid status of a plant. Any treatment which increases the absorption of cations to a greater extent than anions stimulates the synthesis of organic acids (Dijkshoorn, 1963; Joy, 1964; Macdonald and Laties, 1964); this is particularly true of  $\text{K HCO}_3$  the anion of which is an integral part of the metabolic process (Jacoby and Laties, 1971). Conversely, as may be seen as a consequence of salinity, increasing concentration of  $\text{Na}^+$  and  $\text{Cl}^-$  causes a decrease in concentration of other cations, the change in total cations being less than the increase in  $\text{Cl}^-$  and total inorganic anions, and organic anions are decarboxylated in order <sup>to</sup> maintain electrostatic balance (Bernstein, 1961). Macdonald and Laties (1964) generalised that divalent anions increase and monovalent decrease organic acid status so that the equilibrium concentration in roots in different salt solutions decreases in the order  $\text{K}_2\text{SO}_4$ ,  $\text{KCl}$ ,  $\text{CaCl}_2$ . This is clear from the data of Hiatt (1967b and 1968) although as fig. 4,3,2 indicates, in the case of  $\text{KCl}$ , the organic anions status is dependent on concentration. Below the critical threshold of 0,5 me/L organic anions decrease and above it they increase but in both cases the change is stoichiometrically equal to the change in relative absorption of  $\text{K}^+$  and  $\text{Cl}^-$ . From  $\text{CaCl}_2$  solution Hiatt (1968) proposes that  $\text{Cl}^-$  enters the



cytoplasm balanced by  $H^+$  which reduces the pH of the cell sap, shifts the equilibrium of glycolytic reactions and organic acids are decarboxylated through the EMP pathway utilising the  $H^+$  and releasing  $K^+$  to become associated together with  $Cl^-$  with the positive and negative charges on amino acids; hence the organic anion status is reduced.

Torii and Laties (1966a) conclude that synthesis of organic acids in the cytoplasm is the consequence of  $CO_2$  fixation and in vacuolate tissue which is absorbing ions from different salts, decreases in the order  $K_2SO_4$ , KCl and  $CaCl_2$ . Macdonald and Laties (1964) found that  $^{14}CO_2$  fixation increased with concentration of KCl and was greater with  $K_2SO_4$  than KCl from which it could be deduced that the effect is due to absorption of  $K^+$ . The absorption of  $K^+$  is known to be less from  $K_2SO_4$  than KCl and Jacoby and Laties (1971) demonstrated that exchange of  $^{14}CO_2$  is greater than  $^{14}CO_2$  incorporated in net synthesis. It was suggested by Kirkby and Mengel (1967) that reduction of  $NO_3^-$  releasing  $OH^-$  or  $HCO_3^-$  may enhance  $CO_2$  fixation and the poorer growth of tomatoes on  $NH_4-N$  may be due to its effect on cell sap pH with a consequent decrease in  $CO_2$  fixation.. However, Jacoby and Laties (1971) present very convincing evidence that it is not  $CO_2$  as such but rather  $HCO_3^-$  which is the key component in net synthesis of organic acids.

From a dilute solution of KCl, the amount of  $Cl^-$  absorbed is about equal to the amount of amino acid present and  $K^+$  to the sum of amino and organic acids. The amino acids have equal positive and negative charge and are independent of surplus cation or anion absorption (Hiatt, 1968). Organic

and amino acids are dependent upon respiratory metabolism; if this is anaerobic there is an equivalent efflux of inorganic ions to the medium (Hiatt and Lowe, 1967). It is clear that surplus inorganic cations are balanced by organic acids. In grasses and small grain cereals the balance mainly is by malic acid (Van Tuil, 1965; Jacoby and Laties, 1971) but in these species the absorption of monovalent exceeds that of divalent cations. Malic acid tends to be the acid most liable to fluctuation in short time experiments with discs of carrot, beet and potato (Splittstoesser and Beavers, 1964; Macdonald and Laties, 1964; Hiatt, 1968). In spinach and sugar beet leaves oxalic acid is dominant (Van Tuil, 1965; Joy, 1964; Bengtsson *et al*, 1966) and in potato tubers citric acid (Heisler *et al*, 1964).  $\text{Ca}^{2+}$  and  $\text{Mg}^{2+}$  tend to form undissociated salts of oxalic and uronic acids; only 15 and 25 % of the cations respectively in the stems and roots of tomato were in ionic form (Kirkby and Mengel, 1967). In spinach,  $\text{Ca}^{2+} + \text{Mg}^{2+}$  was correlated with the concentration of insoluble oxalate and very little was associated with pectate (Bengtsson *et al*, 1966).

The stoichiometry between the endogeneous synthesis of organic anions and the difference in the cytoplasm between inorganic cations and anions is well established (Jacobson and Ordin, 1954; Dijkshoorn, 1962; Joy, 1964; Van Tuil, 1965; Splittstoesser and Beavers, 1964; Torii and Laties, 1966a; Hiatt, 1967b). Stoichiometry provided some evidence that either differential absorption of cations and anions was controlled by the synthesis of organic acids or organic acid synthesis was a direct metabolic response to electrostatic discrepancy

during absorption or metabolism of N and S. In 1962 Dijkshoorn formally quantified the relationship. Absorption of ions by plants normally is acidic (there being a nominal absorption of  $H^+$  to balance the surplus anions) but internal alkalinity is created by the metabolism of N and S and release of  $OH^-$  or  $HCO_3^-$ . The buffer capacity of plant sap is low and yet no appreciable changes in pH occurs. He concluded that natural plant acids are sufficiently strong to exist purely as their salts at the pH of plant sap and indeed constitute the stoichiometric balance to internal alkalinity. If more organic acids are synthesised,  $H^+$  will accumulate and pH fall; conversely, inadequate synthesis would leave  $OH^-$  or  $HCO_3^-$  unneutralised and pH would rise. The response to the former would be an increase and to the latter a decrease in absorption of basic cations. Inability to respond in this way would mean an abnormally high or low pH and suboptimal conditions for metabolic activity. Any increase in the surplus of cations over inorganic anions in the cytoplasm generally is agreed to be dependent upon the ability of the tissue to synthesise organic acids, as for example,  $K^+$  absorption from  $K_2SO_4$  where  $SO_4^{2-}$  is only slowly absorbed (Torii and Laties, 1966a; Hiatt, 1968). Conversely, Hiatt, (1967b) proposes a system for continued absorption of  $Cl^-$ , supplied with the slowly absorbed cation  $Ca^{2+}$ , the limit of which is imposed by the supply of endogenous  $K^+$  salts of organic acids.

Perhaps the most obvious stimulus to maintain equilibrium is change in tissue pH (Burstrom, 1945; Hiatt 1967a) but this proposal has been rejected by Torii and Laties (1966a) and

Jacoby and Latices (1971) as being of only minor importance between pH 4 and 8. Torii and Latices (1966b) write "In the range of system 2, cation uptake depends on concomitant anion absorption in inverse proportion to the ability of the tissue to synthesise organic acid in response to excess cation uptake. The exchange of a cytoplasmic  $H^+$  ion for an external cation offer no obvious signal for organic acid synthesis. However, if the absorbed cation is delivered to the vacuole together with a cytoplasmic organic anion at the same time that an  $H^+$  ion from the cytoplasm moves to the external solution, the loss of organic acid in the cytoplasm will be sensed and will result in organic acid synthesis to reestablish equilibrium". Developing this theme, Jacoby and Latices (1971) demonstrated that organic acid sythesis and stoichiometry are separable phenomena in vacuolate tissue. The creation of  $HCO_3^-$  by exchange of a cation for  $H^+$  or its absorption is suggested to be the prime stimulant for the organic acid synthesis by PEP carboxylase. It is the transport to and sequestration in the vacuole which then imposes stoichiometry and the removal of the cation from the cytoplasm encourages further absorption from the medium.

As Hiatt (1968) concludes, the kinetics as applied to absorption assumed to be mediated by a carrier mechanism apply equally to a system in which inorganic ion absorption is regulated by organic acid synthesis. It is for precisely this reason that Torii and Latices (1966 a and b) and Jacoby and Latices (1971) assign organic acid sythesis to system 2 (high concentration) absorption which they previously had shown to be rate controlled by tonoplast transport into the

vacuole. Alternatively, Hiatt (1967b) argues that organic acid synthesis is a characteristic of absorption at any concentration even within the range of system 1. The significant fact, however, is that in the range of concentrations used in this study, which generally were well within the range of system 2, the synthesis of organic acids can be assumed to effect a functional balance between the absorption and metabolism of nutrient ions.

#### 4,3,5. Selectivity and affinity

There are conflicting reports on selectivity during absorption particularly towards  $K^+$  and  $Na^+$  when both are available together in solution at high concentration. Excised roots of low salt status generally have been demonstrated to show high affinity for  $Na^+$  at high concentration, the absorption of which is less affected by the anion type than  $K^+$  (Rains and Epstein, 1967). Whole plants also have been shown to display this characteristic (Pearson, 1967). Pitman, (1967) has shown that the pretreatment of plant tissue has a marked effect upon selectivity and roots of high  $Ca^{2+}$  status, show the "Viets effect" and selectivity is reversed in favour of  $K^+$  (Pitman *et al*, 1968). Marschner and Günther (1964) found that the addition of  $Ca^{2+}$  at low concentration increased selectivity in favour of  $K^+$  by decreasing  $Na^+$  absorption and decreasing the efflux of already absorbed  $K^+$ . Reduction in the pore size of the plasmalemma by  $Ca^{2+}$  is said to be responsible and the larger hydrated  $Na^+$  ion (7,9Å compared with the 5,3Å of  $K^+$ ) may then be preferentially excluded (Hiatt, 1968).



Excised roots of high salt status absorb  $\text{Na}^+$  initially more rapidly than  $\text{K}^+$  from mixed solution although selectivity nonetheless is in favour of  $\text{K}^+$ . Later the rate of absorption of  $\text{Na}^+$  falls below that of  $\text{K}^+$  implying a marked increase in  $\text{K}^+$  selectivity with time (Pitman, 1967; Pitman *et al.*, 1968). This change in selectivity with time may be due to fall in sugar level with salt absorption (Pitman, 1967; Hoad and Peel, 1965). There is evidence, however, that metabolic energy may be employed at the plasmalemma in pumping  $\text{Na}^+$  out after absorption in which case a falling sugar level might more easily indicate an increase in  $\text{Na}^+$  status with time. A metabolic pump into the cytoplasm is indicated for  $\text{Cl}^-$  and maybe for  $\text{K}^+$  also (Pierce and Higginbotham, 1970). At low concentration, Leggett and Epstein (1956) demonstrated a high affinity mechanism for  $\text{SO}_4^{2-}$  absorption but whereas its absorption is low at low concentration it is abnormally high at high concentration (Epstein, 1966).

#### 4,3,6. Antagonism and luxury absorption

The terms antagonism or inhibition are aptly applied to competition during the absorption process and transport within a plant of ions of like charge.

Tromp (1967) generalised that a decrease in the rate of absorption of an inhibited ion is related to the rate of absorption and not the concentration of the inhibiting ion. The inhibitor does not completely exclude the affected ion and its absolute decrease is not stoichiometrically equivalent to the increase in the inhibiting ion. Tromp found that the ratio of the inhibited to the inhibitor ion was the same



in different parts of the root even though their absolute concentrations may vary with region, pH and temperature.

Bange (1962) postulated that interactions may occur between different ions during the enzymic breakdown of the ion-carrier complex. Indeed it is on the basis of competitive phenomena that Nissen (1974) rejects Hiatt's hypothesis (see section 4,3,5) of carrier-less absorption in which control is implied by the capacity of a tissue to synthesis organic anions.

Competition between cations in absorption is well known. A high level of available  $K^+$  has been found to reduce absorption of other cations (Smith and Wallace 1956; Huffaker and Wallace, 1958; Ward, 1959; Said 1960; Allsopp, 1965; Laughlin 1966; Will, 1966; Millikan and Hanger, 1966; Crabtree, 1969; Surarex, 1970; Murarka, 1971). A high level of  $Ca^{2+}$  similarly reduces absorption of other cations (Smith and Wallace, 1956; Said 1960; Udovanko et al, 1964; Coic et al, 1966; Epstein, 1966; Naumann, 1966). A high level of  $Na^+$  generally reduces absorption of other cations (Dijkshoorn, 1957b; Bernstein, 1961; Udovenko et al, 1964, Coic et al, 1966; El-Shiekh et al, 1967; Sutcliffe, 1967). Generally cation content of the plant is found to be less when nitrogen is supplied as  $NH_4^+$  (Dijkshoorn, 1957b; Tromp, 1962; de Wit, 1963; Udovenko et al, 1964; Klemm, 1967; Kirkby and Mengel, 1967). In most studies the source of the cation is solution or fertiliser. Henkens (1965) found however, that at a given  $Na^+$  status in the soil, soil  $K^+$  reduces the  $Na^+$  absorption by grass although  $Mg^{2+}$  had no effect. The proximity of  $K^+$  to  $NH_4^+$  in fertiliser granules was found by

Jakobsen (1967) to increase the competition during absorption. There have been cases, however, when the expected antagonism has not been observed or only very slightly (Tromp, 1962; et al, 1966; Dejaegere, 1966; Tinker, 1967). Udovenko et al, (1964) found that competition of other cations changed with time, that of  $\text{Ca}^{2+}$  increasing and  $\text{Mg}^{2+}$  decreasing;  $\text{NH}_4^+$  competition remained constant. In most species  $\text{Na}^+$  is as easily absorbed and competes with  $\text{K}^+$  but potatoes and beans have either a high exclusion mechanism or a low affinity for  $\text{Na}^+$  so that it is  $\text{Ca}^{2+}$  and  $\text{Mg}^{2+}$  which are the competitors of  $\text{K}^+$  (Freeman, 1967).

Almost as well established as cation antagonism is the competition during absorption between nutrient anions. Fertiliser containing  $\text{Cl}^-$  may increase total anion absorption but absorption of  $\text{NO}_3^-$ ,  $\text{H}_2\text{PO}_4^-$  and  $\text{SO}_4^{2-}$  is reduced (Dijkshoorn and Hart, 1957; Corbet and Gausman, 1960; Schmalfuss and Reinicke, 1960; Walker, 1960; Wilcox, 1961; de Wit et al, 1963; Hannemann, 1964; Udovenko and Ivanov, 1965; Murarka, 1971); decrease in  $\text{SO}_4^{2-}$  is greater than  $\text{H}_2\text{PO}_4^-$  because the former is less mobile (Dijkshoorn, 1957b). The  $\text{NO}_3^-$  ion similarly may reduce the absorption of  $\text{Cl}^-$ ,  $\text{H}_2\text{PO}_4^-$  and  $\text{SO}_4^{2-}$  (Walker, 1960; de Wit, 1963; van Tuil, 1965; Kirkby and Mengel, 1967; Murarka, 1971) but the inhibiting effect on  $\text{SO}_4^{2-}$  is less than that of  $\text{Cl}^-$  (Dijkshoorn and Van Wijk, 1967). At low concentration,  $\text{SO}_4^{2-}$  is not inhibited by other anions and its rate of absorption is markedly increased by the presence of  $\text{CaCl}_2$  in a way similar to the 'Viets effect' in the absorption of  $\text{K}^+$  and  $\text{Na}^+$  (Leggett and Epstein, 1955).  $\text{SO}_4^{2-}$  reduced P concentration after tuberisation in potatoes (Wilcox, 1961) and in saline conditions, a heavy application of P fertiliser reduced the %

$\text{Cl}^-$  in the tissue (Rovekovitch and Porath, 1967).

Epstein and Leggett (1954) concluded that  $\text{NO}_3^-$  did not interfere with halide carrier binding sites nor  $\text{Mg}^{2+}$  with those of  $\text{Ca}^{2+}$ . Divalent ions tend to be retained superficially whereas monovalent ions are rapidly absorbed. Shone (1967) notes that this situation leads to a decrease in the activity ratio of monovalent ions and a change in selectivity. The multiphase absorption isotherm (section 4,3,2) is reflected in the stepwise reduction in  $\text{Na}^+$  absorption as the concentration of  $\text{K}^+$  or  $\text{Ca}^{2+}$  ~~increases and that of  $\text{K}^+$  decreases, as  $\text{Ca}^{2+}$~~  increases in the medium (Rains and Epstein, 1967). The pattern of a multiphase system is visible in some of the data from cation replacement series by de Wit et al (1963). Using models of competition de Wit et al deduced that grass species display 2 systems of competition one of which involves inhibition between  $\text{K}^+$ ,  $\text{Na}^+$ ,  $\text{Ca}^+$  and  $\text{Mg}^{2+}$  and another, which was not apparent in a dicot species tested, involving only  $\text{K}^+$  and  $\text{Na}^+$ . The consequence of the 4 cation system is that they are absorbed at approximately equal rates from a mixed solution. Similarly in the 2 ion system,  $\text{Ca}^{2+}$  and  $\text{Mg}^{2+}$  compete equally but independently of the levels of  $\text{K}^+$  and  $\text{Na}^+$ . The  $\text{NH}_4^+$  ion was not featured in the study possibly because of the complication arising over variation in N supply in a replacement series with other cations.

There are many reports of increase in the absorption of an ion of one charge increasing or decreasing the absorption of ions of opposite charge. Perhaps the most frequent observation is the stimulating effect on cation absorption of

$\text{Cl}^-$  (Dijkshoorn and Hart, 1957; Wilcox, 1961; Hannemann, 1964; Noggle, 1966) and the matter has been discussed in section 4,3,3. Conversely cations vary in their 'stimulation' of  $\text{Cl}^-$  absorption, in order of decreasing effect  $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$  and  $\text{K}^+$ ,  $\text{Na}^+$ ,  $\text{NH}_4^+$  (Udovenko and Ivanov, 1965; Ivanov, 1967). Increasing  $\text{NO}_3^-$  increases  $\text{K}^+$  absorption and vice versa (Klemm, 1967; Murarka, 1971) and  $\text{SO}_4^{2-}$  absorption is increased if  $\text{NH}_4^+$  is the source of N when the anion is  $\text{HCO}_3^-$  as discussed in section 4,3,4. Increasing P fertiliser also may increase  $\text{K}^+$  absorption (Udovenko et al, 1964). These examples of stimulation between ions of opposite charge are an expression of the restoration of equilibrium in a situation where the root is subjected to a ready supply of easily absorbed ions, and is the basis of 'luxury' absorption where the tissue concentration is far greater than that required to fulfil the specific biochemical role of any individual nutrient ion. It is an important phenomenon in 2 respects. In saline conditions, the ability of a species to adjust its internal osmotic pressure to that of its environment is a mark of adaptability (Bernstein, 1961). Secondly the absorption of a neutral salt is the compensatory mechanism during N and S metabolism which maintains organic anion concentration and tissue pH constant (Dijkshoorn, 1962). However, Noggle (1966) concluded that growth is likely to be depressed by reduction in the organic anion concentration as a result of excessive absorption from KCl at a lower concentration than that which would cause osmotic damage.

#### 4,3,7. The relevance of short term experiments to field crops

Many of the recent physiological studies quoted in sections 4,3,2 to 4,3,5 have been performed in vitro using

most commonly excised barley roots and sometimes storage tissue<sup>and</sup> leaf slices. Obviously experiments on these tissues are of short-term duration measured in hours. Generally, the characteristics of ion absorption by roots have been detected in other tissues of the plant suggesting that ions delivered to them in the transpiration stream are absorbed by a process similar to that operating in the roots, although the latter is said to be rate limiting (Nissen, 1974). The time factor is important because absorption capacity increases with time (Sutcliffe, 1956; Osmond and Laties, 1967) and the absorption patterns observed before equilibrium has been established may differ fundamentally from that at equilibrium (Hiatt, 1968). Perhaps more relevant to this study is the considerable evidence that whole plants growing for larger periods also may exhibit absorption characteristics similar to excised roots and tissue slices (Joy, 1964; Epstein, 1973; Nissen, 1974). However, Tromp (1962) comparing different experiments with excised roots and intact plants suggests that their absorption isotherms may differ quantitatively, but Sutcliffe (1956) suggests the difference to be qualitative. De Wit et al (1963) regard excised roots as fundamentally different from growing plants because the organic anion concentration in roots is not constant. Lacking a system for the metabolism of N and S, roots lack an essential component in the control mechanism. As mentioned in section 4,3,5 selectivity changes with time (Sutcliffe, 1956; Tromp, 1962; Pitman, 1967; Pitman et al, 1968; Epstein, 1973; Nissen, 1974). That this may occur during the growth of a crop to maturity is indicated in the results of Sutcliffe (1956), and El-Sheikh et al (1971). The reasons may be the fall in the activity ratio of



monovalent ions due to their initially rapid absorption and the superficial retention of divalent ions (Shone, 1967) and fluctuations in the sugar level of tissues (Hoad and Peel, 1965; Pitman, 1967).

An interpretive problem arises in the relationship between ion absorption and growth, that is between the quantity of an ion absorbed (plant content), plant growth, morphological redistribution and tissue concentration. Nissen (1974) describing the results of Fageria and van Hai, who grew rice plants for long periods in nutrient solutions of widely varying P concentration, notes that due to differences in growth the phases of the absorption isotherm could be detected only on the basis of concentration of P and not total P absorption. Kirkby and Mengel (1967) obtained an unequivocal result of differential response of tomato seedlings to  $\text{NH}_4^+$  and  $\text{NO}_3^-$  nutrition only because the former resulted both in a lower concentration of cations and reduced growth; had one characteristic been enhanced by  $\text{NH}_4^+$  nutrition then a dilemma in interpretation may have arisen. The  $\text{Cl}^-$  ion is easily absorbed but is not metabolised and, except at low concentration in certain species, has no specific biochemical function. Rapid absorption of  $\text{Cl}^-$  occurs without an increase in growth and tissue concentration increases not only of the anions but of the accompanying cation too (Dijkshoorn, 1957b). This phenomenon may be enhanced by a reduction in growth following the reduction in organic anion concentration which almost invariably results from KCl nutrition (Noggle, 1966). This does not occur normally with the absorption of  $\text{NO}_3^-$ ,  $\text{H}_2\text{PO}_4^-$  and  $\text{SO}_4^{2-}$  (Dijkshoorn, 1957b), Similarly if one nutrient becomes limiting to growth its



concentration falls whereas that of other nutrients remains constant. Concentration in older tissues often falls because of dilution by structural carbohydrate but there is an overall fall in the rate of nutrient absorption because of depletion of the growing medium and reduced absorption ability of the roots (Watson, 1963). Bremner and El Saeed (1963) found that nutrient uptake per plant is greater at low crop density but if density is increased, removal per plant falls but concentration may increase. Murarka (1971) concluded that as an index of nutritional state of potatoes, uptake data were more useful than concentration and Will (1966) found that although treatment may reduce foliage concentration of certain nutrients, increased growth resulted in their greater uptake. Thus there is the problem of uneven distribution of ions and assimilates within the plant and growth dependent upon more factors than nutrition. Clearly the interrelationship between ions in a plant is the same on the basis of overall concentration and total absorption. The problem arises when comparing treatment effects on different plants and attaching significance to ontogenetic changes. Since change in dry weight is often proportionally greater than change in concentration of ions, perhaps due to the sort of self regulating mechanism proposed by Noggle (1966), significance may be attached to treatment effects on ion absorption whereas in effect they merely reflect variations in growth. If concentration of ions is seen in the context of their requirement for specific biochemical functions, for example a cation required to act with a given concentration of an enzyme, and as contributing to a pH and metabolism regulating

mechanism as proposed in section 4,3,4 or to an osmotic pressure adjusted to the environment, then in terms of growth limiting functions it is concentration and not uptake of an ion which is the significant characteristic.

Assuming yield to be closely related to the absorption of fertiliser ions Nissen (1974) comments: "The relationship between yield and amount of nutrient is generally taken to be a continuous function and is often described by various forms of the Mitscherlich equation in a first order rate differential equation, or polynomial equations. This may not be strictly valid in view of the fact that ion uptake, a process fundamental for growth, is a discontinuous function of the internal salt concentration." This may be so but if no evidence of a discontinuous yield/fertiliser response curve can be found can it be argued that a field crop grown to maturity does not display a multiphase ion absorption isotherm? (The term 'isotherm' is a misnomer in the context of field crops in any case). Perhaps as Nissen (1971) has observed of the comparison of his own and other experiments with excised roots, the question of precision may arise in studies made with field crops. Alternatively as Johanson and Joham (1971) found with excised cotton roots, although absorption occurred in 3 phases as  $\text{Ca}^{2+}$  concentration increased, only the first was related to increased growth.

#### 4,3,8. Solution concentrations and fertiliser experiments compared

The threshold between Epstein's systems 1 and 2 generally

has been found to occur between 0,1 and 1 mM salt solution (see section 4,3,2). Although system 1 is considered to operate at high concentration the absorption of ions is increasingly dominated by the characteristics of system 2 as the solution concentration is increased. The established 'complete' nutrient solutions (for example Hoagland and Long Ashton) have a total concentration of salts well into the range of system 2. Even the concentration of the treatment ions alone in the controlled environment experiments in this study were so high, that the characteristics of system 1 can be ignored (see appendix 10,2,4).

The situation in the field is less easy to anticipate. The analysis of saturation extracts only approximates to the effective concentration of salts in soil solution because of the uneven distribution of ions in the aqueous phase surrounding negatively charged roots and soil particles. Lagerwerff (1965), however, concludes that when equilibrium exists between roots, soil solution and particles then the saturation extract fully characterises the ionic environment. Fertiliser increases root growth and exploration (Watson, 1963) but it may be broadcast or banded and may be distributed down the profile by leaching such that the root environment is far from uniform. The soil solution concentration varies with the moisture content of the soil and with the rate of removal of ions by fixation and absorption by the crop and other organisms. Depletion reduces uptake (Gregory, 1937) and Clutterbuck (1972) found that exchangeable soil  $K^+$  diminished throughout the season.

Asher and Ozanne (1967) quote the concentration of soil solution of  $K^+$  as 0,7 - 1,5 me/L which is greater than that which has been found to sustain growth; exhaustion through the season however, partly is responsible for falling growth rate. In a  $K^+$ -fixing soil of 20000 ppm total K, only 78 ppm was exchangeable and leaching with  $H_2CO_3$  removed only 112 ppm which was less than that absorbed by rye. After removing the equivalent of the exchangeable fraction the concentration of  $K^+$  in the leachate was 2,6 me/L, well below the threshold of system 2 (Williams, 1961).

Following soil fertilisation with  $K^+$ , drilled in bands, it is possible to make some hypothetical calculations of certain 'fixed points'. If the fertiliser is placed in contact with a cylinder of soil and if the nutrient dissolves in the soil water, its concentration before mass action is given by

$$\frac{3,18 RF}{ed w r^2} \quad \text{me L}^{-1}$$

where R is interrow spacing in cm

F rate of fertiliser nutrient in  $\text{kg ha}^{-1}$

e gram equivalent weight of nutrient

d apparent density of soil in  $\text{g cm}^{-3}$

w water content of soil in  $\text{g g}^{-1}$

r radius of cylinder of soil in contact with fertiliser in ~~air~~ band.

The most concentrated solution is the easiest to estimate.

If  $K^+$  is applied in 75 cm rows at the rate of 300 kg/ha to a sandy soil of apparent density 1,7  $\text{g cm}^{-3}$  and water content at wilting point 0,05  $\text{g g}^{-1}$  and no leaching occurs so that the radius of the soil cylinder is 2 cm, then the concentration of  $K^+$  in soil solution would be 5400  $\text{me L}^{-1}$ . According to Reisenauer (1966) few arable soils have a saturation extract

more concentrated than  $5 \text{ me L}^{-1}$  of  $\text{K}^+$ . To this sum must be added any other fertiliser which may be applied, nitrogen salts and other soil ions in solution of which the most important are  $\text{Ca}^{2+}$  and  $\text{Mg}^{2+}$ . Unless the soil dried below wilting point it is unlikely that a potato crop in Scotland would experience a soil solution more concentrated than  $10 \text{ e L}^{-1}$ . A uniform soil solution of this strength would render the soil overwhelmingly saline but a transitory localised concentration of this magnitude would severely damage plant tissue in contact with it (cf. Simpson, 1963).

Reisenauer (1966) found 8% of soils tested had a solution concentration of  $\text{K}^+$  of less than  $0,25 \text{ me L}^{-1}$ . Clearly a leached sandy soil without fertiliser represents another possible extreme, in which case accumulation of ions by a crop clearly would be limited by the characteristics of system 1 absorption. More realistically, assume  $100 \text{ kg/ha}$  of  $\text{K}^+$  is applied to a heavy clay soil of apparent density  $1,2 \text{ g cm}^{-3}$ . Suppose the fertiliser is banded as before but leaching has distributed the fertiliser within a cylinder of soil radius  $20 \text{ cm}$ . If the soil is at field capacity it may contain  $0,45 \text{ g g}^{-1}$  of water and the concentration of fertiliser  $\text{K}^+$  in soil solution would be  $2,8 \text{ me L}^{-1}$ , again within the range of system 2 absorption. If the fertiliser had been broadcast and leached to a depth of  $20 \text{ cm}$  then the concentration of fertiliser  $\text{K}^+$  in soil solution would be  $2,4 \text{ me L}^{-1}$ .

A large proportion of  $\text{K}^+$  would be removed from the solution as fixed and exchangeable ions and non-exchangeable salts, by leaching and, within the first 2 months, by crop

growth. Under these circumstances, the concentration of  $K^+$  in soil solution may be expected to start well within the range of system 2 absorption but absorption of  $K^+$  by a growing potato crop progressively would become influenced by the characteristics of system 1 absorption.

#### 4,4 SUMMARY CONCLUSIONS

4,4,1 A biological system is a dynamic equilibrium between a multitude of interacting processes. Various measurements are made in succeeding chapters which may indicate the state of the processes which lead to the effects of KCl and  $K_2SO_4$  on potatoes described in chapter 3. However, it is unreasonable to expect an unequivocal pattern to emerge of causal relationships.

4,4,2 KCl is more water soluble than  $K_2SO_4$  but it is unlikely that solubility is responsible for the effects. Most of the absorbed  $K^+$  reaches the roots by diffusion. KCl has a higher diffusion coefficient than  $K_2SO_4$  suggesting it to be a more rapidly available source of  $K^+$ . However if KCl increases exchangeable  $Ca^{2+}$  and  $Mg^{2+}$  then it also reduces the free energy difference of  $K^+$ .

4,4,3 There is little other evidence for the effects originating in the soil, whereas there is much to support the differential effects originating during ionic absorption.



4,4,4 A Donnan equilibrium favours the diffusion of relatively more monovalent ions into the free space of the cortex. Absorption into the endodermis is an active process and much disagreement revolves around the mechanisms. Ions enter the cytoplasm and are delivered either into the vacuole or via the symplast of the root into the xylem. A similar process of absorption occurs from the xylem into other tissues.

4,4,5 The largest group of physiologists, generally using excised roots and tissue slices, believe that ionic absorption isotherms are discontinuous multiphase systems, the first at low concentration (system 1) differing fundamentally from subsequent phases (system 2). The threshold between them is a solution strength of between 0,1 and 1 mM. Another group believes that only a single multiphase system exists. A third group replaces the generally accepted carrier theory by an absorption system in which equilibrium is maintained by the synthesis of organic acids. It is clear that the absorption pattern changes with salt concentration in the medium.

4,4,6 System 1 may operate over the complete range of concentration but absorption above the threshold increasingly is dominated by the characteristics of system 2. System 2 absorption may be by diffusion and display Donnan phenomena but selectivity data suggest a more complex explanation.

4,4,7 The maximum rate of absorption varies with the type and age of the tissue and is inversely related to its salt status. The pH of the medium affects absorption rate and the optima may be different for different ions. However, the increase in respiration rate during salt absorption is unlikely to be a controlling mechanism.

4,4,8 Absorption of cations by system 1 is unaffected by the accompanying anion and vice versa. Some authors believe it represents the filling of the cytoplasm and others the limit of the cytoplasmic capacity to synthesise organic acids or supply endogenous  $K^+$  salts of organic acids for decarboxylation. Some reports suggest that system 1 absorption shows a high affinity for  $K^+$ .

4.4.9 In system 2 absorption, suppression of the root membrane negative potential causes an exponential increase in anion absorption rate with increasing concentration. The rate varies with the ion species but mainly with its valency and with the species of the accompanying cation. Conversely the rate of cation absorption is controlled by the absorption rate of the accompanying anion. Some ions in order of rate of absorption are  $K^+ > Mg^{2+} > Ca^{2+}$  and  $HCO_3^- > Cl^-$  and  $NO_3^- > H_2PO_4^- > SO_4^{2-}$ .

4,4,10 Within the range of system 1 more  $Cl^-$  is absorbed from KCl than  $K^+$ , but above the threshold of system 2 the reverse is true. From  $K_2SO_4$  at all concentrations more  $K^+$  is absorbed

than  $\text{SO}_4^{2-}$ . Within the range of system 1, absorption of  $\text{K}^+$  from  $\text{KCl}$  and  $\text{K}_2\text{SO}_4$  is identical but above the threshold the greater rate of absorption of  $\text{K}^+$  from  $\text{KCl}$  increases with concentration.

4,4,11 The equilibrium tissue concentration should reflect the rate of absorption of an ion rather than its concentration in the medium. However, differential absorption may decrease as equilibrium is reached.

4,4,12 The relevance of ratios between the stoichiometric totals of cations and anions largely has been superseded by the more fundamentally meaningful difference between them. The ability of 1 ion to replace another without affecting the stoichiometric total has long been recognised.

4,4,13 Absorption of cations is in exchange for  $\text{H}^+$  and anions for  $\text{OH}^-$  and  $\text{HCO}_3^-$  with the medium. The pH changes in the medium and the equivalent change in the cell sap is dependent upon the differential absorption of cations and anions.

4,4,14 Ions may become associated with amino acids but because they have equal positive and negative charges they cannot accommodate differential absorption.

4,4,15 A net change in the negative potential arising out of N and S metabolism and differential ion absorption would influence the pH - sensitive metabolic processes. At the normal pH of cell sap buffer capacity is low so a sensitive control mechanism is required. This is the role of organic

acids. An excessively high or low organic anion concentration for a given species is presumed to represent stress in such a system.

4,4,16 The synthesis of organic acids is related to  $\text{CO}_2$  fixation but probably it is the appearance of  $\text{HCO}_3^-$  in the cytoplasm which stimulates synthesis. The well-known stoichiometry between organic acids and surplus concentration of inorganic cations over anions, or between the change in organic acid concentration and differential absorption of cations and anions, is said to be due to the transport of the salt of the organic acid and its sequestration in the vacuole.

4,4,17 In graminaceous species malic acid is the main equilibrating acid but in potatoes citric acid also is important. In the leaves, particularly of spinach and sugar beet, and particularly as they age, oxalic acid is functional in this respect. Much of the  $\text{Ca}^{2+}$  and  $\text{Mg}^{2+}$  form insoluble salts of oxalic and uronic acids and are outside the equilibrating mechanism.

4,4,18 There is a fundamental difference in the mechanism for the control of cellular ionic equilibrium between excised roots and growing plants. Differential absorption of cations and anions by the former is balanced by the <sup>n</sup> synthesis or decarboxylation of organic acids. In the latter, N and S are metabolised generally with an endogenous release of net negative charge; this must be equilibrated with differential absorption of cations and anions. It is a unique faculty of

a growing plant that is able normally to maintain organic anions at a constant concentration over a long period of time. In excised roots although stoichiometric balance must be maintained the concentration of organic anions may change rapidly.

4,4,19 Treatments which characteristically increase the organic anion concentration are  $\text{NO}_3\text{-N}$  and  $\text{K}_2\text{SO}_4$  and those which reduce it are  $\text{NH}_4\text{-N}$  and  $\text{CaCl}_2$  ( $\text{KCl}$  is intermediate in effect between  $\text{K}_2\text{SO}_4$  and  $\text{CaCl}_2$  since  $\text{K}^+$  is easily absorbed).

4,4,20 Plants probably absorb  $\text{K}^+$  from low salt concentration selectively. Within the range of system 2 there are conflicting reports of selectivity between  $\text{K}^+$  and  $\text{Na}^+$  but there is evidence that in the presence of  $\text{Ca}^{2+}$  it is in favour of  $\text{K}^+$ . At low concentration  $\text{SO}_4^{2-}$  may be selectively absorbed from a mixture of anions even though its absolute rate is low. Absorbed  $\text{Na}^+$  may be actively pumped out of the cell and  $\text{Cl}^-$  pumped in;  $\text{K}^+$  too may be pumped in.

4,4,21 Antagonism is the competition between ions of like charge during absorption. Ions of like charge generally are mutually competitive although in addition to a 4 ion system involving  $\text{K}^+$ ,  $\text{Na}^+$ ,  $\text{Ca}^{2+}$  and  $\text{Mg}^{2+}$  some plants may display a separate 2 ion system of competition between  $\text{K}^+$  and  $\text{Na}^+$ . Potatoes have a low affinity for  $\text{Na}^+$  so it is  $\text{Ca}^{2+}$  and  $\text{Mg}^{2+}$  which compete with  $\text{K}^+$ . Anions are mutually competitive but  $\text{Cl}^-$  may inhibit  $\text{SO}_4^{2-}$  more than the reverse. The form of N has important implications in competition since  $\text{NH}_4^+$  strongly inhibits other cations and  $\text{NO}_3^-$  other anions. A decrease in

the activity ratio of monovalent ions with time may contribute to the change in selectivity with time.

4,4,22 A rapidly absorbed anion like  $\text{Cl}^-$  increases total cation absorption compared with a slowly absorbed anion like  $\text{SO}_4^{2-}$  but stoichiometry depends on the availability of easily absorbed cations. 'Luxury consumption' of easily absorbed ions enables a plant to adapt to solution environments of different osmotic pressure but the stress on the organic anion system imposed by absorption from concentrated KCl solution may cause depression of growth before osmotic damage occurs.

4,4,23 There is some evidence that at least qualitative similarity exists between the ion absorption pattern of excised roots and growing plants and crops. If this is so then yield may not, as presumed, be a continuous function of fertiliser rate.

4,4,24 Interpretive problems arise from ion absorption by growing plants since growth which may be affected by factors other than ion absorption, and uneven distribution of assimilates and nutrient ions, may confuse the relationship between absorption and concentration of ions. Growth is often affected more by treatment than concentration so that the common correlation between dry matter yield and ionic content is misinterpreted as causal. It is argued that if nutrition is growth limiting then it is more likely to find expression in concentration and not absorption.



4,4,25 The established 'complete' nutrient solutions have salt concentrations well into the range of system 2. Even the treatment ions in the studies reported here are in this range.

4,4,26 From hypothetical calculations relating fertiliser banded for a field crop and soil moisture in which it may dissolve, it seems that in the extreme situation of heavy application to a sandy soil at wilting point, total salt concentration may be very great and osmotically damaging. In the other extreme of a small dressing to a soil of high moisture status then salt concentration may approach the threshold between systems 1 and 2. Depletion during the season may be considerable so that the influence of system 2 becomes progressively less.

#### 4,5 HYPOTHESIS

If the relative effects of KCl and  $K_2SO_4$  fertiliser on potatoes originate in the soil then the reason is most likely to be the more rapid delivery of  $K^+$  from KCl to the roots by diffusion. At the concentration involved more  $K^+$  will enter the root from KCl than  $K_2SO_4$  either by Donnan phenomena or active absorption or both, and more  $K^+$  will be found in all the tissues at equilibrium. Much more  $Cl^-$  will enter the tissues from KCl than  $SO_4^{2-}$  from  $K_2SO_4$  and this will produce a smaller concentration of carboxylate anions. The effect increases with salt concentration so that a heavy rate of KCl is expected to place a stress on the endogenous pH